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Focus and scope

The journal aims to disseminate, to a wide audience, knowledge, information and innovative approaches that promote and enhance the wise use and management of biodiversity in order to sustain the systems and species that support and benefit the people of Africa.

The journal publishes original research findings, as well as reviews, commentaries or perspectives, strategies and short communications. Special focus issues emanating from symposia or conferences that fall within the scope of the journal may also be published.

Authors should contextualise submissions within the framework of the value chain of biodiversity knowledge from its generation, to its application and use. We are especially interested in articles that are written using language and terminology that is accessible to a wide audience.

Specifically, the scope of the journal covers the following areas:

1. Generation of new knowledge that provides a foundation for assessment, planning or management of biodiversity, including new taxonomic discoveries within Africa, from across all Kingdoms of organisms, documenting the abundance, diversity and distribution of genes, species and ecosystems in Africa (including temporal changes in these), and understanding the interactions among components of biodiversity that contribute to the functioning of ecosystems.
2. Assessment of biodiversity, including the status of populations, species and ecosystems, the impacts of threats, harvesting and disturbance or of interventions on populations, species and ecosystems, and the value of the goods and services provided by biodiversity.
3. Innovation in science- or evidence-based decision-making for biodiversity in Africa. This includes the publication of case studies, best practices, tools and plans for the conservation, use and management of biodiversity.
4. Cross-cutting fields specifically developments and innovation in human capital development in the biodiversity sector and innovation in biodiversity information management and dissemination systems and tools for use of biodiversity information.
5. Strategic frameworks that provide guidance and direction for biodiversity research, assessment and management at community, local, national, regional or continental levels, especially those that integrate biodiversity management with local and regional socio-economic systems.

Submissions from authors anywhere in Africa as well as those based outside of Africa are invited if the content relates to African biodiversity.

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The journal meets the criteria of the Department of Higher Education and Training (DoHET). It is therefore accredited and approved by the DoHET for its inclusion in the subsidy system for being a research publication for South Africa.

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Commemorative issue celebrating 100 years of Botany on the Potchefstroom campus of the North-West University: past and present contributions to understand the impact of land-use change on algal and plant diversity in aquatic and terrestrial ecosystems.

Knowledge for a different urban future: a reflection

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Ecological infrastructure of urban regions

What is the role of urban ecosystems and what do we need to know about it? Urban ecosystems jointly woven together into a green infrastructure are central to quality of life of urban residents and for mitigating the environmental impact of the increasingly global plurality known as 'cities'. Cities appropriate more and more of Earth's land surface, either for the built cities themselves (Seto et al. 2011) or for the production systems they need for their survival (e.g. Morgan & Sonnino 2010; Nyström et al. 2019). However, 'cities' and 'urban' are somewhat deceptive terms as they may give the impression of homogeneous units with clear boundaries, which is very far from what they are – cities are characterised by small scale mixes of various land uses – from remnant nature and parks to transportation infrastructure, commercial areas and housing areas (from luxury homes to skyscrapers, and including informal settlements). Further blurring definitions, rural areas are in many ways becoming increasingly urban – people are moving back and forth between cities and the countryside and lifestyles are becoming increasingly similar through increasingly extensive and diffuse peri-urbanisation (e.g. Ravetz et al. 2013). For the most part, the urbanisation in Africa is following similar patterns as elsewhere in the world, but it becomes more distinct due to its extent and its rapid development (Anderson et al. 2013). One significant pattern is the anticipated rapid growth in smaller towns and the generally weak state control, the preponderance of feeble formal economic sectors, strong linkages between cities and rural areas through circular migration, urban remittances that contribute to rural economies, and rural districts where smaller towns expand and form connected 'urban' agglomerations (McHale et al. 2013).

Understanding the urbanisation context and positioning urban biodiversity work (research, restoration, conservation or design) as nested within a larger landscape will thus always be critically important. Quite often cities are located in biodiversity-rich areas (Seto et al. 2012) and promoting regionally embedded and connected urban ecosystems offers ways for – at least to some extent – mitigating habitat and biodiversity loss from urban expansion. It may also help to reduce the indirect impacts cities may have on the environmental quality of the surrounding landscape (e.g. Siebert et al. 2021). When located instead adjacent to homogeneous, intensively used production landscapes, cities and urban ecosystems may offer refugia for organisms that no longer are able to find sufficient habitat qualities in the urban hinterlands. Either way, larger scale connections between the city and its hinterlands are an essential aspect of urban ecology (as captured by urban gradient studies, see e.g. Du Toit et al.

2020). They allow for more exchange and a more dynamic interplay that is important for the long-term development of the ecology of urban regions. Refugia and biodiversity-rich source areas within and outside the city support recolonisation and overall landscape functionality (Lundberg & Moberg 2003). Cities with their global trade connections are also melting pots for novel combinations of biodiversity and may thus be sources of invasive species, which could potentially spread following the same routes (e.g. Hulme 2009). Flows are not limited to human mobility or the movement of other organisms, other geophysical processes reinforce the urban–rural linkages, as perhaps most evident in the flow of water and the many upstream–downstream issues that come with mixes of different land uses (e.g. Barnard et al. 2021).

Not only do cities grow outwards and interact with their surroundings, the urban environment itself is in constant change. Species meet and interact in new ways, forming novel and changeable urban assemblages (Hobbs et al. 2006; Kowarik 2011), climate change is exacerbated by the urban heat island effect, soils are constantly disturbed (Muller et al. 2021), green infrastructure is meshed with buildings and transportation infrastructure and water is rerouted and quite often polluted (Koekemoer et al. 2021). Land conversion and construction of transportation infrastructure or housing may be the most obvious land-use change, but people's actual use and stewardship of land (management practices, recreational uses, preferences for plants or other organisms etc.) will have additional, more subtle but still profound implications (Andersson et al. 2007). South Africa has a relatively long history of studying and documenting aspects of biodiversity and ecosystems through systematic biodiversity assessment (Cilliers et al. 2021). This has resulted in a knowledge base on biodiversity that continues to grow, the identification of linkages between land uses, priority areas and recommendations for biodiversity management and conservation (e.g. Kellner et al. 2021), and assessments of the status and trends of biodiversity as well as environmental quality (e.g. Berner et al. 2021; Muller et al. 2021, Shikwambaba et al. 2021, Siebert et al. 2021). Knowing the causes and likely consequences of change will become increasingly vital as we move into a future characterised by uncertainty and change. This knowledge is also a first step towards building resilience around liveable cities – for people as well as other species. The next step is to understand what it is that makes or could make (since we are not exactly in an ideal situation) them liveable.

Vegetation is the backbone of all urban ecosystems and an interface through which multiple different processes and actors connect. In addition to providing potential habitat for animals (humans included), plants are critically important for the quality and functional character of urban ecosystems. Photosynthesis and evapotranspiration generate biomass and various consumable resources, plants are actively involved in water and nutrient cycling, soil formation and water treatment. Vegetation plays a role in regulating local climate and in stabilising the system during extreme events (e.g. by reducing soil erosion) (e.g. El Kateb et al. 2013). These functions are also directly and indirectly important for our own wellbeing. Humanity is now primarily an urban species, but we are still dependent on the biosphere to provide us with multiple contributions to healthy, meaningful and fulfilling lives. An increasingly rich field describes the links between people and the biophysical world around us, exploring different ways of framing ecosystem services or nature's contributions to people, and thus better articulating and highlighting their role for our wellbeing. Beyond the baseline of our material needs and preferences, nature also contributes to spiritual wellbeing, creativity, sense making, place making and social and cultural life (e.g. Merçon et al. 2019), and exposure to urban ecosystems is for many the most frequent opportunity for realising these benefits. For example, gardens and gardening offer opportunities to, for example, project and reinforce identities, produce medicinal and nutritional products, and enhance aesthetic qualities (e.g. Cilliers et al. 2018). Remnants of less intensively or intentionally managed ecosystems offer opportunities to experience silence, a sense of non-human 'agency', wonder and real-world uncontrollability (e.g. Dixon 2002). These wellbeing outcomes are all grounded in functioning ecosystems, which in turn require healthy, diverse and resilient vegetation.

Stewardship

We need to recognise that people are fundamentally part of urban ecosystems and their resilience, in tangible as well as more abstract ways. Human activities exert pressure on ecosystems and biodiversity, but they are also an integral part of a co-evolutionary process that can be beneficial to urban ecosystems as well as people. Over the last 15 years, stewardship has gained attention as a way of analysing and describing local management, engagement and volunteerism for the sake of the larger environment as well as personal wellbeing, and general attitude and commitment towards the environment (Peçanha Enqvist et al. 2018; Chapin III 2020). Stewardship engagement may come from a need to act out or express care for the environment (e.g. Chawla 1998; Tidball & Stedman 2013). Engaging with and for the urban environment can be a way to reclaim a bond that has been lost. Urbanisation has been highlighted as one of the drivers behind an increasing disconnect between people and the larger environment that we depend on (e.g. Miller 2005). An opportunity to participate and take on responsibility for something larger than yourself and your self-interest can also be empowering; it has been shown that people mobilise to increase their control over the local environment in a context where space is scarce and often contested (Ernstson et al. 2008). The South African Biodiversity Stewardship Programme is a formalised version of stewardship (led by conservation authorities entering into legal agreements with private and communal landowners) (Wright et al. 2018). Management is based on voluntary commitments from landowners, including those in and around urban areas (Holmes et al. 2012), with a range of different types of biodiversity stewardship agreements. However, as studies from around the world show, there are more ways people can be involved in management, decision making and learning about their daily environment (e.g. Wilson 2020). Not least, cities typically have a wide range of actors who influence the landscape in different ways. User interests, access to land and property rights are shared unequally among different groups, which influences their motivation, capacities and stewardship strategies (Colding & Barthel 2013). For example, a comparison of people managing parks, cemeteries and allotment gardens in Stockholm showed that both ecological knowledge and commitment to management varied (Andersson et al. 2007). Urban residents can express a strong sense of care through their engagement in very localised stewardship activities such as gardening (Cilliers et al. 2018), urban foraging (Shackleton et al. 2017) and co-management initiatives (Graham & Ernstson 2012; Colding & Barthel 2013). Different interests are often associated with different capacities to influence governance processes (Baviskar 2003; Swyngedouw 2009). This raises concerns about the terms of participation, equal access and social justice, especially for cities.

A language for learning

One of the prerequisites for successful management – and involvement in management – is knowledge. Urban ecological infrastructure can be an active space for learning. For example, gardens – community gardens, health clinic gardens, botanical gardens, home gardens – can be knowledge hubs and active interfaces for exchange and learning (Cilliers et al. 2018, 2021). They offer opportunities for peer-to-peer learning and transfer of skills as well as higher education. However, knowledge is often compartmentalised, and to combine knowledge from different sources can help make more systemic sense of different specific knowledge. One such bridge could be a different way of describing and discussing biodiversity. In times of change, and to connect ecology with human perceptions and needs, we need an expanded framework for investigating, communicating and sustainably making use of ecological properties. We need to know not only what species are and where they can be found, but what they do and how people perceive them and attribute meaning to them. There is a growing interest in functional traits as a bridge between ecophysiology, ecology and geosciences, and other disciplines more interested in human wellbeing, behaviour and sense making (Andersson et al. 2021). Traits which determine how organisms respond to change are a powerful tool for understanding some of the dimensions of ecological resilience (see e.g. Muller et al. 2021; Van Coller et al. 2021). When combined with traits describing the influence the organisms have on their environment, this approach can provide a baseline for starting to think about the resilience of the functions that in turn support ecosystem services.

Roots of resilience for urban futures

Human wellbeing will benefit from greener cities and urban areas that are designed with a careful eye to ecology. Not all direct contacts between people and a rich biodiversity are positive, not for people and certainly not for other organisms. However, this doesn't mean that we don't need, or cannot accommodate, organisms that we should not interact too closely with. Ecology has its own logic, and many of the processes we are dependent on are complex and will require more biodiversity than we may think, especially if they are to continue to work across different circumstances. Finding a balance in urban designs that supports both desired and necessary biodiversity requires deep knowledge, especially as some elements of a functional ecosystem may be dangerous to people. Universities and research institutes are not the only providers of such knowledge, but they are very important. As the articles in this special feature show, there is knowledge to build on, and knowledge that needs to be made available and actively translated into management action. To end with an alliteration: Knowledge, not least botanical knowledge, can and needs to inform restoration, reconciliation, reclamation, resilience, reconnection and risk reduction.

Disclaimer

The views expressed in the submitted article are the authors' own and not that of his institution. This paper has not been peer reviewed.

Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

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Hundred years of Botany at the NWU: contributions towards understanding plant and algae function, diversity and restoration in a changing environment

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The Department of Botany on the Potchefstroom Campus (formerly Potchefstroom University for Christian Higher Education) of the North-West University (NWU) had its centenary in 2020.

In this paper we celebrate this milestone by giving an overview of the history of the Department at this campus, including its recent establishment and expansion on the NWU Mahikeng Campus (formerly the University of North-West). A brief overview is presented of the advances in teaching and research over the years, and the development and relevance of the important plant collections in the botanical garden, two herbaria and the national diatom collection.

The main emphasis of this contribution is, however, a reflection on the advancement and significance of research conducted by various disciplines on plant and algae function, diversity and ecological restoration over the years.

The different disciplines in Botany at NWU, from the oldest to the more recent, are Plant Taxonomy, Plant Ecophysiology, Terrestrial Plant Ecology, Aquatic Sciences, Urban and Settlement Ecology, Geoecology, and Proteomics.

Different aspects contributing to changes occurring in the environment, such as pollution, land degradation, urbanisation, overexploitation of resources and the subsequent effect of these on plant diversity and function are especially addressed in our current research. The results of our research *inter alia* led to solutions for problems occurring in the landscape and contribute to the well-being of the people using the land and water by restoring important ecosystem services.

Keywords: Aquatic sciences, geoecology, plant ecophysiology, proteomics, taxonomy, terrestrial plant ecology, urban and settlement ecology.

Introduction

The Botany Department of the former Potchefstroom University for Christian Higher Education (PU for CHE) (now part of the North-West University) was 100 years old in 2020. To celebrate this milestone this special issue of *Bothalia – African Biodiversity and Conservation* was initiated. The aim of the present paper is to provide an overview of the 100-year history of the Botany Department and the botanical garden at this institution, and also to highlight research in the different disciplines and their contribution towards knowledge on plant and algae function, diversity and ecology. Most of the current research has focused on addressing the negative effects associated with land-use changes. As this is not intended to be a complete review of each research discipline, only few of the most important research papers are highlighted. The other contributions in this special issue will focus on specific current research projects in the Department.

Brief History of the Department of Botany at NWU

A century ago it was not unusual to find Botany students attending lectures in an old stable in Potchefstroom (Figure 1) on the premises of the house of Marthinus Wessel Pretorius, former president of the South African Republic/*Zuid-Afrikaansche Republiek* (in the 1880s). This is where Botany found its humble beginnings in the earlier years of the PU for CHE. On sunny days, practical classes were conducted under the oak trees (*Quercus robur* L.) in the garden, which are still today silent witnesses of those earlier 'aha!' experiences so typical of studies of the plant kingdom. Botany later moved to the more luxurious, old prefabricated military barracks that were erected on the main university campus in Potchefstroom (Jooste 2017). Subsequently, Botany has since relocated twice, and today has excellent facilities including laboratories, a botanical garden, herbaria, ecological research sites, green houses and open-top growth chambers, all state of the art.

Initially, in 1920, Botany and Zoology courses were presented by one lecturer, but five years later a dedicated lecturer for Botany, Mildred Radloff (Figure 2), was appointed. She had to carry a full load of lecturing and presenting practical classes for all three pre-graduate year groups until 1931 when she married and had to resign due to the protocol of the University at that time. The first professor and head of department was Antonie Goossens (Figure 3) and with his appointment (1932–1961) a new phase started for Botany, with the first master's degree student (Mr W.J. Stapelberg) enrolling in 1933. Goossens was dedicated to develop Afrikaans terminology for Botany and he and a colleague, Piet Botha, published the first comprehensive Botany textbook in Afrikaans, *Leerboek vir Plantkunde*, in 1944, which was used at all the Afrikaans universities until 1971. He also published the first Afrikaans key to the families and genera of flowering plants of South Africa (1940), and compiled the first English–Afrikaans/Afrikaans–English botanical dictionary (1972).

Botha became the next head of department (1962–1972). He specialised in plant physiology under guidance of the renowned plant physiologist Prof Karl Wetzel of the Friedrich Wilhelm University, but due to the outbreak of World War II in 1939, he had to flee Germany. He completed his doctorate through the University of South Africa (UNISA). Another botanist at the PU for CHE who was affected by the war was Max Papendorf (later the third head of department; 1973–1982). He had earlier completed an excellent master's study under Goossens. Papendorf had received the George Grey bursary to study abroad but was prevented by the outbreak of the Second World War (Jooste 2017).

Daan Botha was appointed as the fourth head of department (1983–1985) and he will be remembered for his initiative to change the veld garden into a botanical

Figure 1. First lecture room for Botany – a stable (Source: NWU Records, Archives and Museum).

Figure 2. Miss Millie Radloff, first lecturer in Botany (Source: NWU Records, Archives and Museum).

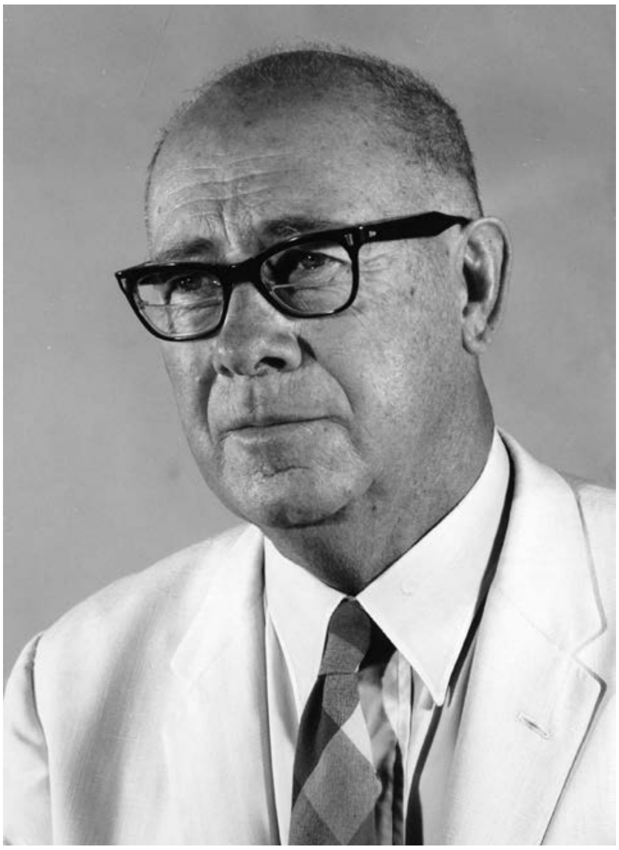

Figure 3. Prof. A.P Goossens, first Professor and Head of Department of Botany (Source: NWU Records, Archives and Museum).

garden, which is now a living legacy. Botha left in 1985 and became the Director of the National Botanical Gardens of the National Botanical Institute (later South African National Biodiversity Institute). His successor, Ockie Bosch (1986–1993), focused on establishing an integrated approach in the teaching of Botany, which culminated in significant changes to the curricula and a name change from the Department of Botany to the Department of Plant Sciences, in accordance to international trends at the time. Five years later another name change followed when Soil Sciences merged with Plant Sciences to become the Department of Plant and Soil Sciences. This led to further changes in the curricula to ensure that plant and soil sciences complemented each other at honours level so that postgraduate students could specialise in resource development, horticultural sciences, pasture ecology or plant pathology. When Braam Pieterse became the sixth head of department (1994–1997), the integrated approach was phased out, and eventually he reinstated the Botany Department with focus on the sub-disciplines of Botany (Jooste 2017).

In 1996 the University embarked on the formation of different Schools and Botany became one of six subject groups in the School of Environmental Sciences and Development. No major changes occurred in the undergraduate courses, but at postgraduate level the focus was placed on Environmental Sciences and botany lecturers contributed to integrated courses in different streams, namely Ecological Remediation and Sustainable Management, Biodiversity and Conservation Biology and Water Sciences. Since 1998, the subject group Botany was led by chairs on a rotational basis (Gert Krüger (1998–2002), Sarel Cilliers (2003–2006 and 2009–2013), Klaus Kellner (2007–2008), Sanet Janse Van Vuuren (2014–2016), Stefan Siebert (2017–2019) and currently Sandra Barnard (2020–). In 2004 the PU for CHE merged with the former University of North-West and the Sebokeng campus of the Vista University to form the North-West University with three campuses (Potchefstroom, Mahikeng and Vanderbijlpark) and eight faculties.

In 2012 the School of Environmental Sciences and Development split into two new Schools and Botany became part of the School of Biological Sciences (Jooste 2017). Postgraduate studies were divided into different subprogrammes and Botany staff and students contribute to Aquatic Ecosystem Health, Biodiversity and Conservation Ecology as well as Ecological Interactions and Ecosystem Resilience (Jooste 2017). In 2017 the Botany subject group expanded to the Mahikeng campus. Subsequently, major changes in the undergraduate courses had to be implemented to align the Botany modules between campuses.

Figure 4. Botanical Garden – Waterfall on Prof. Daan Botha's koppie. (Photo: Chris van Niekerk from NWU Botanical Garden collection).

Although Botany curricula have been changed quite drastically over the years there was always a constant stream of students interested in Botany. Enrolled student numbers averaged 113, 61 and 37 for Botany I, II and III respectively since 2010. Botany has also been phased in successfully on the Mahikeng campus and in 2020 we have enrolled 123, 56 and 55 students for Botany I, II and III respectively. Post-graduate training has always been an important focus for the Botany Department. Over the last ten years, 105 Masters and 25 PhD students were supervised in different disciplines of Botany at the NWU.

Both past and current alumni are well known names in the South African Botany community. The list is long and here we list only those with postgraduate degrees from the department who became professors at other universities – Manie van der Schijff, Albert Eicker, Braam van Wyk (all Pretoria), Kobus Eloff, Braam Pieterse, Amie van der Westhuizen (all Free State), Jan de Bruin, Johan Visser, Frikkie Botha, Anna-Maria Botha (all Stellenbosch), and Ockie Bosch (University of Queensland, Australia) (Jooste 2017). Botany alumni are also employed outside academia in various sectors (often in senior positions) – Agricultural Research Council, Department of Environment, Forestry and Fisheries, Eskom, MidVaal Water Company, North-West Province Agriculture, Rand Water, South African Environmental Observation Network, South African National Biodiversity Institute, South African Sugar Research Institute, and various botanical gardens, private environmental consultation firms and NGOs.

Brief History of the NWU Botanical Garden

The origins of the NWU Botanical Garden (Figure 4) may be traced back to 1925, when Radloff was appointed as the first Botany lecturer at the Potchefstroom University. She was responsible for the collection of fresh plant material for practical sessions, and the Botanical Garden would eventually grow due to this need for plant material – and it remains one of the key functions of the garden to this day.

However, it was several decades later, in the early 1960s, that the first steps were taken by Goossens to initiate a garden. At the insistence of Goossens, Wynand Louw was appointed in 1962 as a taxonomist and Botany lecturer, and one of his first tasks was to develop

Table 1. Founders and curators of the plant collections of the Potchefstroom and Mahikeng campuses of the North-West University since 1932

Curator	Period	Years	Collection
Antonie P. Goossens[F]	1932–1961	29	Herbarium of the PU for CHE (PUC)
Wynand J. Louw	1962–1970	8	PU for CHE Veld Garden
Daniel J. Botha[G]	1971–1985	14	Herbarium of the PU for CHE (PUC)
Bert Ubbink	1973–1990	17	PU for CHE Botanical Garden
Sello D. Phalatse[F]	1983–2008	25	University of North-West Herbarium (UNWH)
Gideon F. Smith	1986–1992	6	Herbarium of the PU for CHE (PUC)
Daniël J. Theunissen	1993–1997	4	Herbarium of the PU for CHE (PUC)
Matthias H. Buys[B]	1998–2006	8	A.P. Goossens Herbarium (PUC)
Peter Mortimer	2003–2006	3	North-West University Botanical Garden
Stefan J. Siebert	2007–present	14	A.P. Goossens Herbarium (PUC)
Martin F. Smit	2007–2011	4	North-West University Botanical Garden
Jonathan C. Taylor[B]	2009–present	11	South African National Diatom Collection (SANDC)
Pieter W. Malan	2009–2016	7	University of North-West Herbarium (UNWH)
Christiaan J.G. van Niekerk	2012–present	9	North-West University Botanical Garden
Madeleen Struwig[B]	2017–present	4	S.D. Phalatse Herbarium (UNWH)

[F]Founder, [B]Renamed collection, [G]Founder of the botanical garden

a garden to grow plant material for practical classes. Louw identified a piece of land in the northern part of the campus and started to develop a veld garden to supply fresh plant material over the next eight years, until 1970, when he left the university.

The idea to develop a proper botanical garden came in 1971, with the appointment of Daan Botha as plant taxonomy lecturer and curator of the herbarium (Table 1). In 1972 he appointed the garden's first horticulturist, Derick Pitt, to help with the development and maintenance of the garden. Pitt left the garden within a year after his appointment and Bert Ubbink, a horticulturist from the University of Pretoria, was appointed as the first permanent curator of the garden in 1973. Ubbink was responsible for the design, layout and construction of the pathways and the water ponds throughout the garden.

During the early 1990s, the University drastically reduced funding of the Botanical Garden and there was a shift in focus to more integrated teaching and research. The maintenance of the Botanical Garden was transferred to the campus garden services and the Garden curator was redeployed to the Technical Services Department on campus. This was the start of a period of tragic neglect of the Garden. Over the next decade, the Garden and buildings deteriorated to a state of dilapidation and an overgrown piece of veld.

The recovery and revival of the Botanical Garden started in 2003 with the appointment of a new curator, Peter Mortimer. Under the leadership of Mortimer, the deteriorated structures were repaired, unwanted trees were removed, and new flower beds were designed and constructed.

After the aforementioned merger of universities in 2004, Annette Combrink, rector of the Potchefstroom campus, recognised the important role of the Botanical Garden for community education, capacity building, and for promoting the image of the NWU. Martin Smit succeeded Mortimer as the Garden curator (2007–2011), and he sourced funds through Combrink to further improve the Botanical Garden. Smit and his team made huge improvements to the garden design and layout (Smit et al. 2011). The current curator of the Garden, Chris van Niekerk, was appointed on 1 November 2011, and is implementing Smit's vision to expand the plant collections and to make the Botanical Garden a multi-disciplinary experience. To achieve this the garden added a geological display in a geological rock garden representing a walk back in time through rocks exposed in the 2023 million year old Vredefort meteorite impact structure and a site-specific digital literature experience called 'Byderhand'.

The living plant collection in the Garden represents species from 105 families. Rare species such as *Brachystelma barberae* Harv. ex Hook.f., *Clivia mirabilis* Rourke, *Prototulbaghia siebertii* Vosa, *Searsia batophylla* (Codd) Moffett and *Welwitschia mirabilis* Hook.f., serve as reference collections for research projects (Berner et al., 2020). The Garden not only supports training and research of students within the NWU, but it also focusses on *ex situ* conservation of various species. More than 2000 individuals of the endemic *Khadia beswickii* (L.Bolus) N.E.Br. (Van Niekerk & Siebert 2018) and various other species of special interest, such as *Boophone disticha* (L.f.) Herb. and *Nananthus vittatus* (N.E.Br.) Schwantes, have been rescued, relocated and monitored due to destruction of their natural habitat.

Different Research Disciplines in Botany

Plant taxonomy

Plant taxonomic research at the Potchefstroom campus dates back to the early 1930s. The first taxonomic work was conducted by Antonie Goossens (Figure 2) who focussed on grasses from the Potchefstroom region. This eventually led to the description of the genus *Bewsia* Gooss. (Goossens 1941) and several grass species new to science, for example *Anthephora argentea* Gooss., *Enneapogon spathaceus* Gooss., *Sporobolus bechuanicus* Gooss., *Styppeiochloa gynoglossa* (Gooss.) De Winter, *Tarigidia aequiglumis* (Gooss.) Stent and *Urochloa stolonifera* (Gooss.) Chippind. (Goossens & Philips 1932). The Herbarium of the PU for CHE was founded by Goossens in 1932. The herbarium was later renamed in his honour by the sixth curator, Matt Buys (Table 1), and officially became the A.P. Goossens Herbarium. Today it holds over 30 000 specimens for educational and research purposes.

In the 1960s, Wynand Louw succeeded Goossens as taxonomist and discovered many new species of succulents, of which *Euphorbia louwii* L.C.Leach commemorates his life-long dedication. From 1970 to mid-1980s, Daan Botha was the resident plant taxonomist and under his supervision various taxonomic studies were conducted on a range of genera, such as *Antizoma* (Menispermaceae), *Brachylaena* (Asteraceae), *Crabbea* (Acanthaceae), *Eugenia* (Myrtaceae), *Sphedamnocarpus* (Malphigiaceae) and *Vitex* (Lamiaceae). Various taxonomic changes were proposed (e.g. Bredenkamp & Botha 1993). Gideon Smith succeeded Botha in 1986, and like Louw, was a succulent devotee with a research interest in the Asphodelaceae, Crassulaceae and Mesembryanthemaceae (now Aizoaceae), which subsequently led to the revision of several genera in later years. Both Botha and Smith moved on to head up directorates at the National Botanical Institute (later South African National Biodiversity Institute).

During this period the University of North-West herbarium (UNWH) was established in Mahikeng by David Phalatse (Figure 5). He established the herbarium in 1983 as a teaching facility for the Biology Department at the then University of Bophuthatswana. This herbarium became part of the University of North-West and later the North-West University during the amalgamation in 2004. With the introduction of Botany as subject on the Mahikeng campus in 2017, it was incorporated into the subject group of Botany and was renamed the S.D. Phalatse Herbarium by the third curator, Madeleen Struwig (Table 1). The collection is fast approaching 1 000 specimens and will be expanded considerably to meet the educational and research demands of the Mahikeng campus. Like the A.P. Goossens Herbarium, it also serves as a voucher repository for various disciplines studying plants, their products and applications beyond pure botanical studies.

In the mid-1990s, Danie Theunissen combined his ecological and taxonomical knowledge to identify grass ecotypes for application in agriculture and rehabilitation, which culminated in a range of ecosystematic accounts of ecotypes in grass genera such as *Digitaria*, *Eragrostis*, *Setaria* and *Themeda* (Theunissen 1992). Matt Buys was taxonomist from 1998 to 2006 and had a keen interest in the genera *Lobostemon* (Boraginaceae), for which he described various new taxa, and the phylogeny of *Delosperma* (Aizoaceae). Under his supervision the genera *Drimiopsis* (Hyacinthaceae) (Lebatha et al. 2006), and *Ruschia* (Aizoaceae) were revised. He is currently the curator of Scion's National Forestry Herbarium in New Zealand.

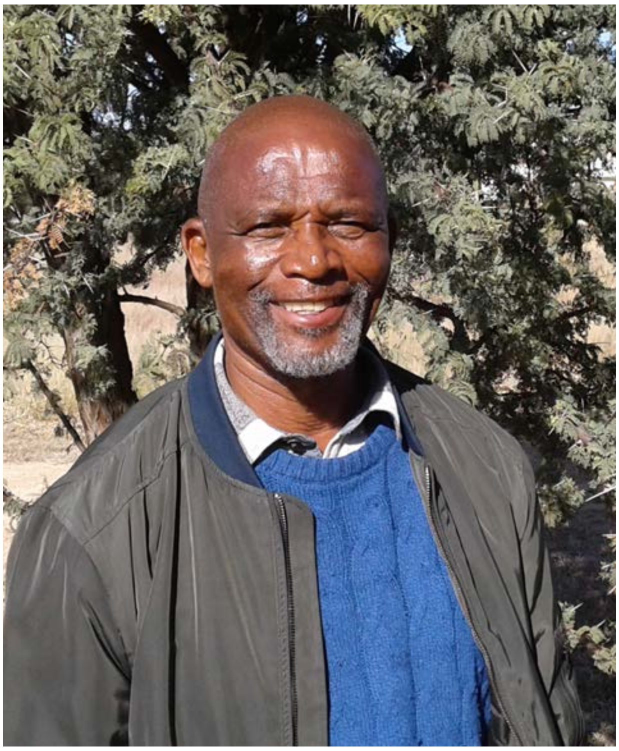

Figure 5: Mr Sello D. Phalatse, first Botanist at Mahikeng Campus (1983–2008), founder and curator of the University of North-West Herbarium (Source: NWU Records, Archives and Museum) (Source: NWU Corporate Relations and Marketing).

Since 2007 taxonomic work has mainly focussed on *Boerhavia* and *Commicarpus* in the Nyctaginaceae (Struwig & Siebert 2013). The two genera were revised for the first time in southern Africa and resulted in the description of a new species, *B. orbicularifolia* Struwig, and a new variety, *C. squarrosus* (Heimerl) Standl. var. *fruticosus* (Pohn.) Struwig (Struwig & Siebert 2013). Floristic studies have also led to the description of rare and endemic species from Sekhukhuneland in Limpopo (Siebert et al. 2010), such as *Euclea sekhukhuniensis* Retief, S.J.Siebert & A.E.van Wyk (Ebenaceae), *Pavetta glaucophylla* Retief, S.J.Siebert & A.E.van Wyk (Rubiaceae), and *Polygala sekhukhuniensis* Retief, S.J.Siebert & A.E.van Wyk (Polygalaceae). With the advent and development of Botany as a subject on the Mahikeng campus in 2017, taxonomic research has gained momentum under Struwig and various revisions are currently underway on members of the Molluginaceae.

To strengthen taxonomic research at the NWU, two extraordinary lecturing appointments were made of taxonomists employed by the South African National Biodiversity Institute. Pieter Bester was appointed to the Potchefstroom Campus from 2013 and Marinda Koekemoer to the Mahikeng Campus from 2019. Bester is an expert on the Apocynaceae and Koekemoer on the Asteraceae. Their knowledge of the diagnostic characters of plant families, and development of educational material for use in practical plant identification have greatly contributed to the training of undergraduate students studying the flora of South Africa.

Taxonomy at NWU has contributed to the national effort to categorise and name plants. The major focus has been on the Poaceae, and specialist interest in the Apocynaceae and Nyctaginaceae (Bester & Nicholas 2018, Struwig & Siebert 2013). The specific focus on grasses in both herbaria has enabled other botanical fields studying land-use change in the Grassland and Savanna biomes to identify and measure character traits of the fundamental units of biodiversity, namely the species. The A.P. Goossens Herbarium holds an actively utilised, ornamental plant collection of close to 2 500 specimens originating from an urbanisation gradient stretching from rural villages to the Johannesburg metropole. It also keeps large ecological voucher collections (> 20 000 specimens) of the Potchefstroom region to Vredefort Dome (both the Dry and Mesic Highveld Grassland Bioregions), Ganyesa to Griqualand-West (Eastern Kalahari Bushveld Bioregion), and Dwarsberg to Impala Platinum (Central Bushveld Bioregion). In recent years, taxonomists on both campuses have contributed to new research in Botany that focuses on the taxonomical and functional trait diversity of forbs across land-uses in grassy biomes (Siebert et al. 2021). To support this initiative, a large collection of forbs from the Lowveld Bioregion has been collected over a decade.

Plant ecophysiology

Piet Botha established the plant physiology discipline in 1937. The theme of Botha's PhD degree from the University of South Africa was the biology of the plant parasite *Alectra vogelii* Benth. (Botha 1950). He was the director of the Institute for Plant Physiological Research at PU for CHE, which was established in 1949, and which later became the Institute for Botanical Research in 1970. Charles Whitehead (appointed as lecturer/associate professor in 1977) investigated ethylene sensitivity in plant tissues to elucidate the mechanisms involved in the control of senescence and ripening in plants with the view to develop effective methods to delay senescence and ripening of fruits and vegetables (Whitehead et al. 1984).

Since the appointment of Gert Krüger in 1988, the focus of research in plant physiology was directed at studying the physiological and biochemical basis of the response of crop plants and natural vegetation to environmental stress. The research, with an integrative approach, involved studying plant responses on a reductionist as well as on a whole-plant level, ideally suited to the teaching of the principles of plant physiology. The key feature facilitating research on plant responses was the outstanding laboratories for the study of the ecophysiology and biochemistry of photosynthesis, and facilities to grow plants under strictly controlled conditions, such as a state-of-the-art open-top chamber facility (OTC) (Figure 6) for studying air pollution effects.

In an endeavor to determine the physiological parameters that could be used as drought tolerance selection criteria for different tobacco cultivars, the effect of induced drought was studied in depth through its effect on photosynthetic gas exchange (Van Rensburg & Krüger 1993a), oxidative stress metabolism, accumulation of secondary metabolites such as proline and abscisic acid (Van Rensburg & Krüger 1993b) and osmoregulation, by postgraduate student and later Research Director: Unit for Environmental Sciences and Management, NWU, Leon van Rensburg. During this time supportive research on the anatomical and cytological anomalies found in studies of water stress on plants was done by Hester Kruger.

Pioneering studies on the application of prompt chlorophyll *a* fluorescence induction for assessing photosynthetic potential and vitality of test plants subjected to environmental stress were undertaken in close collaboration with the international expert on chlorophyll *a* fluorescence kinetics, Reto Strasser, University of Geneva. By analysing fluorescence transients of plants exposed to different light regimes according to the so-called JIP-test, deconvoluting the behavior of PSII into several functional and structural parameters, it was demonstrated that these parameters undergo differential changes upon a particular stress. The JIP-test is now

Figure 6. State-of-the-art open top chambers for research in ecophysiology (Photo: Jacques Berner).

used all over the world and the paper by Botany staff is regarded as a standard document (Krüger et al. 1997). Further technical developments of the JIP-test were illustrated by several papers on chilling stress in soybean.

Riekert van Heerden joined the department as plant physiologist in the mid-1990s and his doctoral studies on various aspects of chilling stress in soybean culminated in several key publications. With the aim to identify the traits that convey dark chill stress tolerance various approaches were employed, such as determining the effect of separately and simultaneously induced dark chilling and drought stress on photosynthesis, the monitoring in parallel of CO_2-assimilation, O-J-I-P chlorophyll fluorescence kinetics and nitrogen fixation of test plants, and assessing the constraints on Calvin-Benson cycle metabolism (Van Heerden et al. 2003). An outstanding practical outcome of the chilling stress research was the ranking of chilling tolerance in soybean genotypes probed by the O-J-I-P chlorophyll fluorescence transient (Strauss et al. 2006).

During the period 2002–2008 several investigations on the effect of air pollution on natural vegetation and crop plants were undertaken. This work was initially done in collaboration with the Helmholz Environmental Research Centre, Leipzig-Halle, Germany and the Atmospheric Chemistry Research Group of the North-West University. Various publications appeared on subjects such as the constraints on photosynthesis of C_3 and C_4 crop plants by trichloroacetic acid and the effect of fluorinated hydrocarbons on C_3 and C_4 crop plants (Smit et al. 2008). Studies using OTCs included the physiology of SO_2 injury and the interaction thereof with drought stress in soybean, comprising the measuring of effects on photosystem II structure and function, photosynthetic gas exchange, *Rubisco* activity, water relations and nitrogen fixation (Heyneke et al. 2012). The constraints imposed by elevated levels of tropospheric ozone on crop plants were also studied employing the OTC system. Being able to, in addition, regulate the CO_2 concentration of the air in the OTCs allowed assessment of the effect of elevated atmospheric CO_2 concentrations to obtain insight into the effects of increased atmospheric CO_2 levels associated with global warming (Maliba et al. 2019).

Jacques Berner joined Botany as plant physiologist in 2007. Currently, the research of Berner is directed towards the acclimation strategies of new climate resilient crops, like quinoa and amaranth. Prompt fluorescence and modulated 820 nm reflection are extensively used to evaluate biotypes with stress tolerance. His skills for the study of the ecophysiology of plants *in vivo* and *in situ*, were also successfully applied in studies on environmental stress exerted on plants of the Namib Desert (Krüger et al. 2017; Berner et al. 2021).

Terrestrial plant ecology

Ecological studies began in 1963 after Koos van Wyk completed his PhD and started with research on degradation of pastures. In 1979 he founded the Institute for Ecological Research with external funding that focused initially on the rehabilitation of road verges, but later also on mine tailings. This institute went through a number of name changes and was terminated under the name Research Institute for Rehabilitation Ecology (Eco-Rehab) in 2005. From 1982 to 1988, George Bredenkamp did extensive phytosociological research on grasslands and savannas and several papers were published from this research (e.g. Bredenkamp et al. 1989; Bredenkamp & Bezuidenhout 1990).

After the appointment of Ockie Bosch as the head of the Department in 1986, the focus was to develop an integrated approach so that all the disciplines in Botany functioned as a unit to encourage collaboration between all scientists in studying community ecology in a dynamic environment.

Johan Booysen, a computer modeler and systems ecologist, joined the Department in 1990. He integrated the community ecology thinking of Bosch into a user friendly computer program to study how the changes in the environment due to climate and management impacts lead to land degradation. This program was named the Integrated System for Plant Dynamics, which required inputs from all sections of Botany, but especially the plant and agricultural ecologists (Kellner & Booysen 2000).

The models of Bosch focused on the influence that management practices have on natural and agricultural ecosystems. To promote sustainable land management, the research focus was on systems ecology, and in collaboration with EcoRehab, it became possible to also address the restoration of degraded rangelands.

Klaus Kellner was appointed at the PU for CHE in 1988 to carry out research on land degradation and rehabilitation ecology in arid- and semi-arid regions of South Africa. He also represented South Africa as the Science and Technology Correspondent (STC) in the Committee for Science and Technology, a subsidiary body of the United Nations Convention to Combat Desertification (UNCCD), served as president of the STC and represented the African continent at the UNCCD. He was also appointed by the UNCCD to global committees regarding the study of the impacts and control of Desertification, Land Degradation and Drought (DLDD), as well as what technologies can be implemented to restore/rehabilitate these lands. This included the *ad hoc* Working Group on Scientific Advice (AGSA), which was formed to identify strategies to bridge the gap between rangeland scientists and policy makers working in the environment (Akhtar-Schuster et al. 2016). DLDD research in terrestrial ecology excelled at NWU and many post-graduate studies and projects followed for government departments in South Africa. International collaboration with organisations from Germany, Namibia, Spain and other European Union countries followed, regarding rangeland restoration after the control of woody shrub encroachment (bush encroachment) in arid- and semi-arid rangelands (Harmse et al. 2016). Although the initial projects were broad, they soon focused more on the western parts of South Africa, as well as the southern parts of Namibia and Botswana (Kellner et al. 2018). Pieter Malan of the Mahikeng campus collaborated with expertise in bush encroachment and restoration after the control of woody invasive species.

Research on land degradation and restoration ecology was extended to include aspects of climate change and the socio-economics of the land users applying sustainable land management, especially in the Kalahari region (Kellner & Bosch 2003). One of the main aims of the UNCCD is to develop a land degradation neutral world, which means that the land that is prone to desertification should be restored after detailed monitoring of the parameters causing the degradation or desertification (Von Maltitz et al. 2019).

Research on grassland and savanna ecosystem dynamics and resilience was expanded from 2012, when Frances Siebert joined Botany. Her relationships with South African National Parks and the Ndlovu (i.e. savanna) node of the South African Environmental Observation Network supported long-term vegetation monitoring in Lowveld savanna. These projects led her to identify the need for an improved understanding of the ecology of forbs, a neglected plant life-form in savanna and grassland (Siebert & Dreber 2019), as they are often perceived as weeds and indicators of land degradation. Forbs, however, provide important forage stability to a wide array of herbivores (Siebert & Scogings 2015). This research has put her on the forefront of international networks working on this topic. She has initiated a forb ecology research consortium with research partners from Brazil, Germany, the Netherlands and national associates, which has led to inclusion in other international working groups, such as the Tropical and Sub-tropical Savanna Plant Functional Traits working group, the International Grassland Restoration working group and the Grazing Exclosure Consortium.

Aquatic Sciences

Aquatic research in Botany includes algal diversity in relation to water quality parameters, including inorganic and organic pollutants. This research focus was established at the former PU for CHE by Braam Pieterse in 1994. At that stage the aquatic research team consisted of Pieterse and four postgraduate students, namely Sanet Janse van Vuuren, Antoinette Vermeulen, Annelie Swanepoel and Danie Traut. Initially, aquatic research primarily focused on the diversity of algae and environmental variables influencing their growth and succession in the Vaal River system (Janse van Vuuren & Pieterse 2005). Over time, especially with the appointment of aquatic scientists from other institutions, the research expanded to include other river systems, dams, and various other habitats throughout the country, and also other research subjects within aquatic sciences.

During 1995, Janse van Vuuren was appointed as junior lecturer in the Department of Botany. Although her early-career research focused primarily on the taxonomy, diversity and ecology of phytoplankton in various freshwater systems throughout the country, she was later also involved in studies of algae in water purification plants, the development of harmful algal blooms (HABs) and aerophytic algae growing against cave walls. Her research culminated in a book on the identification of common freshwater algae (Janse van Vuuren et al. 2006), as well as two chapters in a book on freshwater life (Griffiths et al. 2015).

Sandra Barnard joined the water research group as a lecturer in the Department of Botany in 1996. She initiated a physiological and molecular biological focus in the existing research on algae and this approach later formed an integrated part of aquatic research at the NWU (Conradie & Barnard 2012). Barnard also published research papers about water quality and pioneered research to predict the dynamics and potential of HABs (Van Ginkel et al. 2007; Swanepoel et al. 2016). International cooperation, including a successful student exchange programme, was established between South Africa and Finland (2002–2005).

During 2000, Arthurita Venter completed her PhD on *Oscillatoria simplicissima* Gomont – a potentially toxic cyanobacterium that often forms blooms in South African freshwaters. She was later appointed as an administrative officer in Botany and continued to author several papers on the diversity of algae and cyanobacteria not only in aquatic, but also terrestrial environments (Venter et al. 2013). She is currently considered as a pioneer in understanding the biodiversity of biological soil crusts found on serpentine and mine tailings in South Africa (Venter et al. 2018).

Jonathan Taylor became interested in algae when he first studied these organisms during his first year Botany lectures at the PU for CHE in 1997. His interest eventually led to postgraduate studies in Phycology (the study of algae), during which he became interested in a particular group of algae, the diatoms, which are excellent bio-indicators of environmental conditions. As part of his PhD thesis he tested the application of diatom-based pollution indices, developed for northern hemisphere conditions, in southern hemisphere waters. This led to several publications about the application of diatoms as water quality indicators in South Africa (e.g. Taylor et al., 2007). Today Taylor is known for his work on the taxonomy and ecology of the diatoms from central and southern Africa. He described or contributed to the description of three new diatom genera, 19 new diatom species and three new red algal species. In addition, several diatom species have been named in his honour, namely *Luticola taylorii* Levkov, Metzeltin & Pavlov, *Nitzschia taylorii* Alakananda, Hamilton & Karthick, and *Muelleria taylorii* Van de Vijver & Cocquyt.

Taylor is also curator of the South African National Diatom Collection (SANDC) (Table 1) that was started in 1950 by Béla Cholnoky from the University of Pretoria, later from the Council of Scientific and Industrial Research (CSIR). Other well-known phycologists who contributed to the diatom collection were Robert ('Archie') Archibald, Ferdinand Schoeman (both students of Cholnoky) and Malcolm Giffen (University of Fort Hare). Over the years the national collection also received donations from many scientists abroad and thus contains not only South African material but a large selection of material from around the world. The CSIR donated the collection to the South African Institute for Aquatic Biodiversity (SAIAB) in 2009 to ensure its long term preservation. SAIAB, in turn, has loaned the collection to the NWU in an open-ended agreement (Taylor et al. 2011) as the NWU was becoming a centre for diatom studies (especially taxonomy) in the mid-2000s. The collection, now lodged in the Botany department, has since its move been actively digitised, further catalogued and the type material of many South African species has been investigated. The SANDC is now also a registered herbarium.

Anatoliy Levanets, originally from the Ukraine, joined the research team as a postdoctoral fellow from 2003 to 2006. His experience and knowledge about the diversity of soil and other terrestrial algae complimented existing research on aquatic algae, and it led to several studies on the role that soil algae fulfill in the rehabilitation of mine dumps. The effect of various land-uses, such as effluents of mines containing high metal concentrations, directly influences the morphology and diversity of algal species and therefore research on this subject is extremely important. As part of their studies Levanets and Taylor described three new terrestrial diatom species (*Microcostatus schoemanii* Taylor, Levanets, Blanco & Ector, *M. cholnokyi* Taylor, Levanets, Blanco & Ector and *M. angloensis* Taylor, Levanets, Blanco & Ector) from South Africa (Taylor et al. 2010). In addition to his interest in terrestrial algae, Levanets is also interested in a particular group of freshwater green algae (desmids) and he published an annotated and illustrated list of desmids of southern Africa (Levanets & Van Rensburg 2011).

Information presented in the previous paragraphs illustrates the wide scope of freshwater and algal related research within the subject group Botany. Freshwater research at many other universities is limited, as most are situated in coastal areas and focus more on marine algae and marine research.

Urban and settlement ecology

This research discipline was initiated in 1998 with the completion of the PhD thesis of Sarel Cilliers on the phytosociology of the city of Potchefstroom under the supervision of George Bredenkamp. This was the first-ever study on the description of plant communities in different land-use areas in an urban setting in South Africa. At that time no other ecologist at any African university was interested in the ecology of urban open spaces. Publications from this thesis described plant communities in land-use areas such as vacant lots, intensively managed areas, railway reserves, natural and semi-natural grasslands and woodlands, wetlands and roadside verges. The paper on roadside verges (Cilliers & Bredenkamp 2000) was the most influential publication of all of them. These studies also formed the basis for mapping urban biotopes (habitats) in Potchefstroom to provide ecological data for conservation-orientated planning and management of urban open spaces (Cilliers et al. 2004). Moreover, the Tlokwe City Council used these biotope maps in the development of the spatial development framework of the city.

This initial start led to a focus on the investigation of plant diversity patterns and processes in small and medium-sized cities. Two clear directions were followed, namely fragmented natural grasslands along an urbanisation gradient using a landscape ecological approach, and home and community gardens along socio-economic gradients. Firstly, a Master's degree student, Marié du Toit refined a methodology developed in Melbourne, Australia to quantify the urbanisation gradient in Klerksdorp (Du Toit & Cilliers 2011). This approach was widely used in other studies at the NWU and also globally. Du Toit later completed a PhD and also a postdoctoral fellowship at the NWU. Important findings from the fragmented grasslands research have indicated that urban grasslands are as important as natural grasslands for conservation as they both play an important role in the fine-scale landscape functioning of grasslands (Van der Walt et al. 2015). Research on the dynamics of these grasslands also indicated that despite any current sign of biotic homogenisation they are facing potential extinction debts (Du Toit et al. 2020). Moreover, this study also showed that the indigenous forb species diversity is declining indicating that better management, including urban grassland restoration, is necessary (Du Toit et al. 2020).

Secondly, the growing awareness of the importance of gardens in the urban green infrastructure led to several postgraduate studies under the supervision of Stefan Siebert and Sarel Cilliers. These studies focussed on biodiversity conservation and the provision of ecosystem services that contribute towards human health and well-being. Subsequent publications focussed on garden diversity patterns and their drivers in deep-rural, rural, peri-urban, urban and metropolitan areas. Of these, a paper on the importance of socio-economics as drivers of plant diversity of gardens (Lubbe et al. 2010) was regarded as one of four key papers in a recent global study, which included a meta-analysis of publications on the relationship between socio-economic inequality and biodiversity. Other garden studies included investigations on garden layout and design, the provision of ecosystem services and the potential to study community gardens (e.g. health clinic gardens) in the North-West province as complex social-ecological systems to enhance resilience in a changing world (Cilliers et al. 2018).

Consequently, a large database was amassed on local urban plant diversity. The expertise developed in this research group have led to an intensive involvement in several international collaborative studies with researchers from several universities in Australia, Brazil, Chile, Finland, Germany, Hungary, Sweden, UK and USA. Two global networks that this research group is actively involved in are Urban Biodiversity Network (UrBioNet) and Global Urban Soil Ecology and Education Network (GLUSEEN). UrBioNet, is a global biodiversity network that supports urban biodiversity research, monitoring and practice in three working groups, namely social-ecological linkages, urban biodiversity patterns and traits, and urban biodiversity monitoring and planning (urbionet.weebly.com). GLUSEEN focuses on the study of urban soil ecological systems (www.gluseen.org). As part of this network a comparative study was completed on soil biodiversity and soil decomposition in public green spaces, ruderal areas, remnant natural areas and natural areas in five cities in four countries (including South Africa). From both networks several leading papers were published (e.g. Aronson et al. 2016; Epp Schmidt et al. 2017).

Furthermore, this research group is also involved in transdisciplinary research and training in collaboration with urban planners and landscape architects locally and globally. The main focus is on green infrastructure planning and several projects such as the value of urban green areas and the importance of ecosystem services in planning and design have been completed (e.g. Ahern et al., 2014). Research on these issues has also led to the development of a booklet for the SA Cities Network suggesting ways of guiding future green infrastructure planning and management in South Africa (www.sacities.net).

New specialisation fields: Geoecology and Proteomics

Botany at the NWU has its roots in the study of plant morphology, plant physiology, plant ecology and plant diversity. With the appointment of Stefan Siebert as curator of the herbarium in 2007, this scope broadened to include phytogeography. This research interest allowed him to collaborate since 2010 on interdisciplinary biodiversity projects, primarily for the South African National Biodiversity Institute and the South African Environmental Observation Network. He specifically investigated how the diversity and distribution patterns of plants and arthropods are altered when ecosystems are exogenously disturbed in agricultural, mining and urban environments (Lubbe et al. 2010; Siebert et al. 2021). During this time he also established geoecology as a new research field at the university. Extensive collaboration with Nishanta Rajakaruna (California Polytechnic State University) and Marthie Coetzee (Geology subject group, NWU) through the National Geographic Society has led to various research projects involving geobotanical surveys (Boneschans et al. 2015), heavy metal accumulation by plants (Siebert et al. 2018) and biological soil crusts (Venter et al. 2018) on ultramafic rocks. He has expanded his research to include lichens and is currently studying the interactions of plants with other rock types, such as banded ironstone, dolomite and gypsum.

The establishment of Botany on the Mahikeng campus of NWU in 2017 has strengthened the subject group's expertise in plant biology and biotechnology. Oziniel Ruzvidzo and Tshegofatso Dikobe have a strong research interest in plant proteins. Proteomics is therefore the youngest research discipline in Botany at the NWU. They collaborate internationally with the University of Perugia (Italy), and the Whenzhou-Kean University (China). Specifically, their work on adenylate cyclases is important as these enzymes are increasingly recognised as essential parts of many plant processes including biotic and abiotic stress responses (Chatukuta et al. 2018). It is increasingly clear that plant genomes encode numerous complex multi-domain proteins that harbour functional adenylyl cyclase. These proteins have well-documented roles in plant development and responses to the environment. Hence, Botany staff on the Mahikeng campus conduct research to better understand the intramolecular mechanisms that govern the cellular and biological functions of these proteins (Ruzvidzo et al. 2019). The findings of their work have vast applications in agriculture.

Conclusions

For the past 100 years Botany at the NWU contributed considerably to varied research and development disciplines. From the discussion of the research undertaken over the years it can be seen that the focus was initially on plant physiology and plant systematics, and plant ecology has been included since 1963. Over the last two decades more emphasis has also been placed on different sub-disciplines in ecology studying natural, degraded and anthropogenic ecosystems in terrestrial and aquatic environments. Botany teaching and research at the NWU (and the former PU for CHE) has over the years and is currently playing a major role in the development, and contributing to the prestigious status, of Botany in South Africa. Researchers at NWU are local and international leaders in their specific fields of expertise in e.g. plant function, diversity, taxonomy, aquatic ecology, urban ecology, land degradation and ecological restoration of natural and disturbed terrestrial and aquatic ecosystems. Scientists from various disciplines are also actively involved in collaborative national and international research and development projects and forums. It has always been a priority at NWU to keep a good balance between basic and applied science within curricula and research.

NWU biological scientists have been and are involved in projects and programmes to better understand land-use changes due to natural (e.g. climate) and anthropogenic (e.g. management) impacts. Indigenous plant diversity is mostly diminished and plant distribution patterns altered when land-use change is enforced by people to meet their developmental and economic needs. Research results indicated that land-use changes dilute the trait redundancy of ecosystems and the extent of ecosystem services that can be provided by affected ecosystems. Recent studies on herbaceous dynamics, with a specific focus on forbs, contributed to an improved understanding of ecosystem resilience in areas exposed to land-use change, especially sub-tropical grasslands and savannas. Different ecological restoration methods have been developed and tested in arid- and semi-arid natural rangelands and implementing them improves vegetation condition, contributes to increased grazing capacity and enhances sustainable land management practices. Urban ecological studies have contributed to knowledge of the ecosystem services provided by the urban green infrastructure and assist in the development of a conservation-oriented planning, design and management approach in South African cities. Research on rivers has indicated that their water quality is modified by activities and processes in the water and in the surrounding catchment area and directly influence phytoplankton and benthic assemblages. Furthermore, research results have also contributed to the development and application of diatom indices for routine riverine water quality biomonitoring and the establishment of the South African Diatom Index (SADI), which reflects land-use changes and pollution events in South African rivers. Plant ecophysiological investigations quantified the impacts of elevated carbon dioxide, air pollution and drought stress on crops and native plants.

Research in Botany at the NWU also contributes immensely to the improvement of the health and well-being of South Africans from different cultural groups and socio-economic statuses. Monitoring of species functional diversity and patterns in natural and degraded ecosystems is allowing us to determine when land-use change negatively affects ecosystem functions and the services they provide to humans. It prompts for action to address the subsequent degradation and to put in place mitigation measures to restore the lost functions and services. Studying urban areas as complex and adaptive social-ecological systems enables us to address the specific ecosystem service needs of all residents, working towards the development of climate- and food-resilient cities, towns and settlements. Research on the ecology and functioning of forbs in grassy ecosystems aims to secure future ecosystem goods, services and functions. Forbs as a plant group are important for forage stability during dry seasons, pollinator resources for food security and biodiversity. Research has also contributed to the sustainable use of the large component of forbs that are traditionally used for medicine and/or food items for rural livelihoods. By understanding changes in phytoplankton and benthic assemblages of our rivers, and biomonitoring of water quality using inexpensive methods, a rapid response to pollution events enables management interventions leading to improved river water quality. Local communities can therefore be protected from the nuisance of toxins produced by harmful algal blooms and water treatment plants can produce safe drinking water. From ecophysiological studies it is possible to identify and introduce alternative climate-resilient crops, which may in future provide the much-needed food and nutrient security for sub-Saharan Africa.

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Authors contributions

All the co-authors wrote sections of the paper. SC wrote sections and was responsible for integration of all the sections and coordination of the paper.

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The influence of land use–impacted tributaries on water quality and phytoplankton in the Mooi River, North West Province, South Africa

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Background: Effluents from agricultural activities, metal and peat mining, urban and industrial areas, informal settlements and wastewater treatment plants all influence tributaries feeding the Mooi River. All these land uses ultimately result in a deterioration of water quality in the Mooi River.

Objectives: The main objective was to relate the effects of inflowing tributaries to water quality and phytoplankton assemblages in the Mooi River.

Method: Physico-chemical environmental variables were compared with water quality objectives and known limits to assess general water quality in the Mooi River over a one-year period. Water quality and phytoplankton in tributaries were compared to that at sites upstream and downstream from their inflows to determine the extent to which the tributaries affected the Mooi River. Multivariate analysis assisted in the interpretation of phytoplankton and physico-chemical data at the different sites.

Results: Seven phytoplankton phyla were identified in the Mooi River. Diatoms and green algae were most dense and diverse. Cyanobacteria were responsible for various problems, especially in the Wasgoedspruit where they dominated and reached high densities. Lowest phytoplankton density and diversity were found in the upstream and downstream sections of the river, while maximum density and diversity were found during summer in the middle reaches. The inflow of tributaries, especially the Wasgoedspruit, had a pronounced effect on water quality downstream. Phytoplankton density and diversity were less affected than chemical variables, especially nutrient concentrations.

Conclusion: Various land use activities surrounding the Mooi River's tributaries contributed to a deterioration of water quality in the main stream of the Mooi River.

Keywords: algae, anthropogenic activities, cyanobacteria, eutrophication, nutrients, physico-chemical variables, trophic status

Introduction

In the dry North West Province of South Africa rivers and dams are extremely important as surface water sources. The Mooi River and its three major dams (Klerkskraal, Boskop and Potchefstroom dams) are located in the North West Province, and serves as domestic, agricultural and irrigational water resources for the city of Potchefstroom and surrounding areas. The Mooi River forms a tributary of the Vaal River, one of the largest rivers in South Africa. High summer temperatures, low and unevenly distributed rainfall, and high evaporation rates contribute to insufficient water availability at times (Van der Walt, Winde & Nell 2002).

It is generally accepted that the Mooi River, which literally means 'beautiful river', obtained its name from its once beautiful, clear stream of water. However, the Mooi River currently experiences severe land use impacts in its catchment, affecting water quality in terms of pollution. Surface water pollution, as a result of various anthropogenic activities, is common in the catchment of the Mooi River and includes effluents from agricultural, urban, industrial and recreational activities, as well as from informal settlement areas (NWDACE 2008).

Upstream from Potchefstroom, land-use activities include agricultural activities, diamond diggings, and peat mining. During agricultural activities, which include extensive irrigation, pesticides, herbicides and fertilisers are fed into the aquatic environment (Pelser 2015). According to the World Wide Fund for Nature (WWF 2011), an overuse of synthetic fertilisers, pesticides and herbicides will pollute water resources, poison delicate ecosystems and expose farmers and farm workers to toxins. Diamond diggings in areas surrounding the Klerkskraal Dam (Van der Walt et al. 2002), as well as near the confluence of the Mooi and Vaal rivers, destroy floodplains and remove riparian vegetation, thereby reducing habitat integrity and influencing the associated biota (Currie 2001; Van der Walt et al. 2002). Peatland drainage does not contribute to point sources of pollution but influences the quality of receiving waters with respect to increased sedimentation, nutrient limitation, dissolved oxygen, organic carbon and the release of heavy metals, such as mercury, with its subsequent accumulation in fish and other biota (Glooschenko 1990).

Downstream from Potchefstroom, pump stations of the wastewater treatment plant (WWTP) have the potential of overflowing into the Mooi River. The WWTP of Potchefstroom treats sewage and discharges effluents back into the Mooi River, ensuring that it does not pose threats to human health and the ecosystem (Pelser 2015). However, during high rainfall the plant may overflow and there is a possibility that untreated/semi-treated effluents may be washed into the Mooi River.

All these anthropogenic activities in the catchment contribute to pollution with nutrients such as inorganic nitrogen (nitrites, nitrates and ammonium) and phosphorus (orthophosphates). Phytoplankton (cyanobacteria and algae) is dependent on the availability of nutrients; however, excessive amounts will stimulate their growth and reduce water quality (Sen et al. 2013). Some cyanobacteria can cause serious problems because of their ability to form blooms that result in scums covering the water's surface, creating aesthetically unacceptable conditions, taste and odour problems, as well as toxin production. Decomposition of blooms results in anoxia, causing fish kills (Janse van Vuuren & Taylor 2015).

The Mooi River is further impacted by the inflow of several tributaries, which are influenced by anthropogenic activities in their catchments. The two main tributaries are the Wonderfonteinspruit (WFS) and Loopspruit (LS) (Currie 2001). In the WFS, mining and WWTPs are the main contributors to pollution (Le Roux 2005). Acid mine drainage and heavy metal (uranium) pollution are major water quality concerns (Coetzee, Winde & Wade 2006). The WFS enters the Mooi River just upstream from Boskop Dam, which supplies drinking water to Potchefstroom. Gold mines, located between WFS and LS, also discharge effluents into LS (Van der Walt et al. 2002). The LS is further influenced by agricultural activities and irrigation effluents. Wasgoedspruit (WS), a smaller tributary, joins the Mooi River in Potchefstroom and contains effluents from the polluted Poortjie Dam, industrial effluents from Potchefstroom, as well as urban and storm water runoff. All these effluents enter the Mooi River without prior treatment (Pelser 2015).

The main stream of the Mooi River has been well studied in terms of a variety of subjects related to water chemistry and biota. Research on water chemistry includes the effects of mining (Coetzee et al. 2006) and heavy metal pollution, especially uranium (Winde 2010), contaminants in sediments (Fosso-Kankeu et al. 2015), distribution of inorganic contaminants (Manyatshe et al. 2017), as well as some studies on general water quality aspects (Labuschagne 2017). A diverse assemblage of biota was studied in the main river, including bacteria (Jordaan & Bezuidenhout 2015), cyanobacteria and algae (Venter et al. 2013), macroinvertebrates (Erasmus & De Kock 2015), fungi such as yeasts (Van Wyk 2012) and Hyphomycetes (Van der Merwe & Jooste 1988), plant communities (Du Toit, Du Preez & Cilliers 2021), riparian birds (Luyt 2018), frogs (Kruger 2014) and fish (Van Heerden et al. 2006). However the effect of the water quality of inflowing tributaries on the water quality of the main stream is still unknown.

Taking into account the variety of land uses surrounding the tributaries, especially mining activities in the catchment of the WFS as well as industrial effluents with high conductivity levels entering the WS (personal observation), it was suspected that the tributaries should have a major impact on water quality, and phytoplankton density and diversity in the main stream.

The main aims of the study were therefore to investigate spatial changes in physico-chemical variables, and phytoplankton density and diversity in the Mooi River, and to relate it to the effect of inflowing tributaries. Furthermore, physico-chemical variables were compared to known limits and recommended water quality objectives. This represents the first study on the influence of tributaries on the water quality and phytoplankton dynamics of the Mooi River.

Materials and methods

Study area

The Mooi River originates near the town of Derby (Boons area) and flows southwards into the Klerkskraal Dam (Figure 1). Several natural springs north of Klerkskraal Dam also contribute to flow volume in the upper Mooi River. In general, water quality in the upper section of the Mooi River, from its origin to the Klerkskraal Dam, is excellent because it's not directly influenced by any land use impacts (Le Roux 2005).

The entire WFS is surrounded by active as well as old, abandoned mines and it joins the Mooi River 31 km downstream from Klerkskraal Dam, near the Gerhard Minnebron (GM) Eye. The GM Eye is an active spring, forming part of a huge underground karst network that extends well into the upstream catchment of the WFS (Winde 2011). Peat is mined in a wetland south of the eye (Le Roux 2005).

Boskop Dam is located 7 km downstream from the confluence of the Mooi River and WFS. Potchefstroom with its growing population, university and large industries depends on Boskop Dam for potable water (Van der Walt et al. 2002). From Boskop Dam, the Mooi River flows into the Potchefstroom Dam, located approximately 12 km downstream. Originally Potchefstroom Dam's main purpose was for irrigation, however, in recent years it also became popular for recreational activities.

The WS obtains water from Spitskopspruit and Poortjie Dam on the western side of Potchefstroom. From Poortjie Dam, water flows through a wetland that may act as a filter of pollution (Du Toit et al. 2021). After leaving the wetland, water flows through the industrial area of Potchefstroom, after which the stream bed is converted into a concrete-lined canal that joins the Mooi River approximately 3 km downstream from Potchefstroom Dam.

The Mooi River then flows southwards through Potchefstroom to its confluence with LS on the city's outskirts. Downstream of the confluence, the Mooi River flows past the WWTP where treated effluents are recycled into the Mooi River. From here, the Mooi River flows 25 km southwest, until it joins the Vaal River.

Eight sites, subjected to different sources of pollution, were selected along the Mooi River (Table 1). In

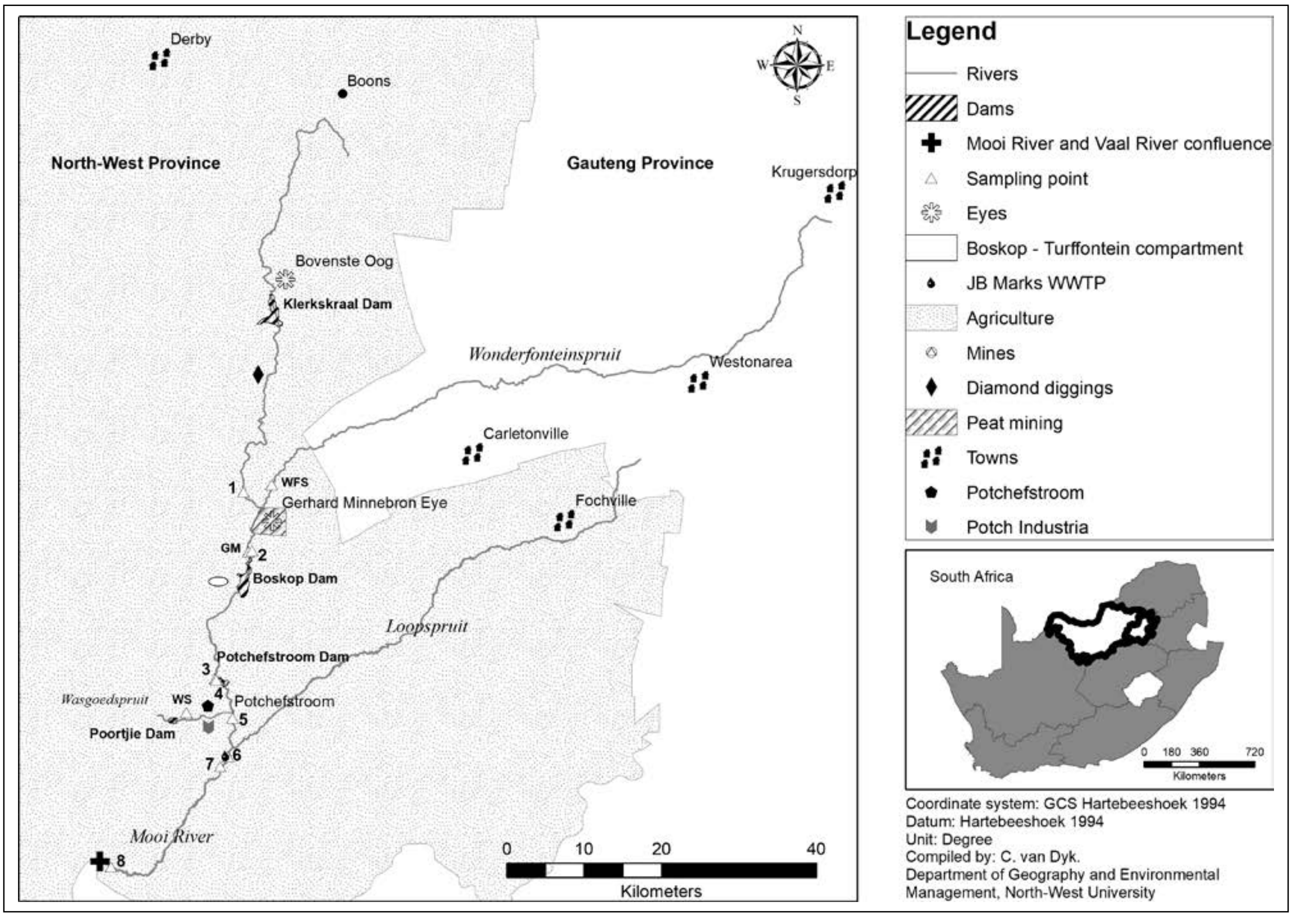

Figure 1: Catchment area of the Mooi River from its source to the confluence with the Vaal River, showing the position of sampling sites in the main stream (1–8) and in the tributaries (WFS, GM and WS). Different types of land use activities in the catchment are also indicated on the map.

Table 1: Sampling sites in the Mooi River and its tributaries, showing possible factors influencing them, their coordinates, as well as the distances and cumulative distances between the sites in the Mooi River main stream

MOOI RIVER

Site no.	Site name	Site mainly affected by:	Coordinates		Distance between consecutive sites (km)	Cumulative distance (km)
1	Upstream Boskop Dam	• Agricultural activities (specifically feedlots, fertiliser pollution) • Diamond diggings	26°26′42.25′′S	27°7′6.02′′E	-	0
2	Boskop Dam Inlet	• Inflow and effect of the Wonderfonteinspruit • Agricultural activities	26°30′52.52′′S	27°7′28.34′′E	± 10	± 10
3	Boskop Dam Canal	• All upstream pollution mentioned above • Dust containing pollutants originating from an ammunition manufacturing company	26°39′44.32′′S	27°5′7.69′′E	± 15	± 25
4	Potchefstroom Dam	• All upstream pollution mentioned above, especially agriculture between Boskop and Potchefstroom Dam	26°39′48.20′′S	27°5′11.54′′E	± 0.16	± 25.16
5	Retief Bridge	• Inflow and effect of the Wasgoedspruit tributary • Industrial, urban and storm water runoff from Potchefstroom	26°42′28.40′′S	27°6′19.87′′E	± 5	± 30.16
6	South Bridge	• The cumulative influence of all activities upstream and in Potchefstroom • Contributions of the Loopspruit tributary	26°45′9.40′′S	27°6′1.19′′E	± 4.5	± 34.66
7	Downstream Final Effluent	• An instant lawn company, located near this site, using fertilisers on lawns • JB Marks waste water treatment plant	26°45′50.44′′S	27°5′29.00′′E	± 1.5	± 36.16
8	Kromdraai	• Agricultural activities, including farming, grazing, fertilizing • Irrigation	26°52′49.48′′S	26°57′51.55′′E	± 25	± 61.16

MOOI RIVER TRIBUTARIES

Site no.	Site name and abbreviation	Site mainly affected by:	Coordinates		Distance between consecutive sites (km)	Cumulative distance (km)
WFS	Wonderfontein-spruit (WFS)	• Mining activities (heavy metals) • Untreated sewage leaks • Effluents from informal settlements	26°26′11.18′′S	27°9′4.03′′E	-	-
GM	Gerhard Minnebron (GM)	• Possible mining pollution from WFS via underground compartments • Peat mining	26°30′4813′′S	27°7′41.59′′E	-	-
WS	Wasgoedspruit (WS)	• Untreated and illegal industrial effluent discharges • Urban and storm water effluents • Sewage spills • Phospho-gypsum mining	26°42′31.44′′S	27°2′19.80′′E	-	-

addition, one site was selected in each of the following tributaries: WFS, GM and WS.

Sampling and analytical procedures

Phytoplankton sampling dates coincided with physico-chemical sampling and analyses done by the JB Marks Municipality, Potchefstroom. Physico-chemical water quality data were obtained from the municipality. Sampling was done in the mornings, starting upstream and ending downstream, just before the confluence of the Mooi and Vaal rivers. At each site a 100 ml surface sample was collected on a monthly basis from January to December 2015. Two millilitres of 37% formaldehyde (formalin) solution were added to each sample to preserve the phytoplankton.

In the laboratory, each sample was shaken vigorously to ensure even distribution of phytoplankton cells. Each sample was transferred to a metal container, and a mechanical hammer, applying a pressure of 49.56 kPa, was used to pressure-deflate the gas vacuoles of cyanobacteria. Depending on the phytoplankton density and concentration of suspended material, a known volume of water (50 or 100 ml) was filtered through a cellulose nitrate filter with a pore size of 0.45 μm to concentrate the phytoplankton cells for counting. The filter paper with phytoplankton was transferred to 10 ml tubes filled with distilled water. A vortex mixer was used to remove phytoplankton from the filter paper, re-suspending the cells into 10 ml distilled water. Depending on the phytoplankton density, 1–6 ml of the sample was extracted with a Finn pipette and transferred to Utermöhl sedimentation chambers. The sedimentation chamber was filled with distilled water and it was covered with a circular glass cover slip to avoid evaporation. Sedimentation chambers were placed in a desiccator for at least 48 hours (24 hours settling time per cm length of the sedimentation tube) to allow the phytoplankton to settle to the bottom.

After two days phytoplankton was identified to genus level using an inverted Zeiss light microscope (at a maximum of 400× magnification) and a variety of literature such as Janse van Vuuren et al. (2006), John, Whitton and Brook (2002), Taylor, Harding and Archibald (2007), and Wehr and Sheath (2003). The transect counting technique, described by Lund, Kipling and Le Cren (1958), was used for phytoplankton enumeration. For colonies and filaments, individual cells were counted as separate entities. The phytoplankton data, initially captured over a 12-month period, was averaged on a quarterly basis to present the data in seasonal format as follows: December–February (summer), March–May (autumn), June–August (winter), and September–November (spring).

Statistical analysis of data

Statistical analyses on phytoplankton and physico-chemical environmental data, as well as the compilation of area and pie charts, were done using STATISTICA 13.3 (StatSoft, Inc. 2017). Kolmogorov-Smirnov and Lilliefors tests for normality were used. The natural log (ln) of the phytoplankton data was determined and used in the statistical analysis. Canonical Correspondence Analysis (CCA) was performed using CANOCO 4.5 (Ter Braak & Prentice 1988) to determine the relationships between distribution of phyla and related environmental factors and gradients.

Results

A summary of the physico-chemical water quality data, in the form of descriptive statistics, is presented in Table 2. Minimum, mean and maximum values, as well as standard deviations and number of samples analysed, are indicated in Table 2. Resource Quality Objectives (RQO) and Resource Water Quality Objectives (RWQO) are also included in this table. Physico-chemical variables include the concentration of inorganic nutrients (ammonia, nitrate and orthophosphate). Turbidity, total dissolved solids (TDS), electrical conductivity (EC), the concentration of a variety of major ions, and pH were also measured.

Results on phytoplankton are presented in Table 3. Seven phytoplankton phyla were found in the Mooi River, as well as at the three sites located in the tributaries. The Bacillariophyta (diatoms) and Chlorophyta (green algae) were most dense (cells per ml) and diverse (number of genera present). The Cyanophyta (cyanobacteria) was less diverse, but also reached high densities. These three phyla succeeded one another as the dominants. A comparison of the different sites revealed that maximum diversity was found in the middle reaches of the main stream (64 genera at Site 4, 60 genera at Site 3), while minimum diversity was found at Site 2 (48 genera).

Interesting observations were made regarding the spatial distribution of genera in the Mooi River and tributaries. *Nostoc, Placoneis*, *Chlorolobion* and *Microspora* were present at the uppermost site of the Mooi River (Site 1), but absent further downstream, as well as from the tributaries. *Aphanothece* was only present in the middle reaches of the main stream. *Staurosira* and *Pediastrum* were absent at Site 1 in the Mooi River, but present in the downstream reaches. *Tryblionella, Carteria* and *Treubaria* were found in the Mooi River but were absent from all tributaries. Genera found in the tributaries, but not in the Mooi River, included *Hippodonta* and *Pandorina* (WS) and *Gonatozygon* (GM).

Table 2: Summary of the descriptive statistics for the physico-chemical environmental variables determined at all sites during the study period January to December 2015. The column shaded in light blue contains the overall descriptive statistics for the Mooi River (values of tributaries excluded in calculation). The columns containing the descriptive statistics of the tributaries (WFS, GM and WS) are shaded in purple. The Resource Quality Objectives (RQO) and Resource Water Quality Objectives (RWQO) set of numerical limits for the different variables are listed in the last two columns. Values exceeding both limits are highlighted in red, and values exceeding one limit, but not the other are highlighted in yellow. Values lower than both limits are highlighted in green. SD = Standard Deviation. - = No limits or data for the particular variable

Variables, abbreviations and unit	Descriptive	Mooi River	Site 1	WFS	Site 2	GM	Site 3	Site 4	WS	Site 5	Site 6	Site 7	Site 8	RQO limit	RWQO limit
Ammonia (NH_3^+) mg/l	Valid N	96	12	12	12	12	12	12	12	12	12	12	12		
	Mean	0.39	0.12	0.17	0.20	0.24	0.17	0.28	1.12	0.83	0.74	0.49	0.29	-	0.03
	Minimum	0.00	0.03	0.01	0.00	0.00	0.01	0.02	0.22	0.03	0.03	0.02	0.04		
	Maximum	4.60	0.32	0.56	0.70	0.82	0.54	1.11	5.16	4.60	3.80	1.23	0.74		
	SD	0.67	0.09	0.18	0.21	0.24	0.17	0.30	1.36	1.29	1.12	0.34	0.24		
Nitrate (NO_3^-) mg/l	Valid N	96	12	12	12	12	12	12	12	12	12	12	12		
	Mean	0.45	0.43	0.41	0.31	0.71	0.28	0.48	1.12	0.49	0.43	0.73	0.43	-	0.3
	Minimum	0.00	0.00	0.10	0.10	0.30	0.10	0.10	0.20	0.10	0.10	0.10	0.20		
	Maximum	3.50	3.30	0.70	0.50	1.10	0.50	3.50	2.80	2.80	0.90	1.50	0.90		
	SD	0.57	0.91	0.20	0.12	0.24	0.14	0.96	1.00	0.75	0.35	0.43	0.24		
Orthophosphate (PO_4^{3-}) mg/l	Valid N	96	12	12	12	12	12	12	12	12	12	12	12		
	Mean	0.68	0.42	0.34	0.47	0.54	0.33	0.36	1.02	0.72	0.65	1.39	1.09	≤ 0.125	0.4
	Minimum	0.01	0.09	0.09	0.05	0.05	0.01	0.03	0.02	0.03	0.05	0.25	0.21		
	Maximum	3.75	1.26	0.69	1.66	1.06	0.81	1.49	5.23	1.77	1.75	3.75	2.28		
	SD	0.65	0.36	0.22	0.46	0.32	0.27	0.41	1.52	0.49	0.48	1.01	0.69		
Total Dissolved Solids (TDS) mg/l	Valid N	96	12	12	12	12	12	12	11	12	12	12	12		
	Mean	475.05	270.25	496.08	473.92	558.42	462.92	475.00	402.18	502.50	533.92	560.75	521.17	-	370.5
	Minimum	208.00	208.00	162.00	419.00	472.00	282.00	391.00	226.00	425.00	440.00	476.00	294.00		
	Maximum	850.00	297.00	660.00	517.00	707.00	850.00	842.00	662.00	647.00	850.00	741.00	692.00		
	SD	121.68	23.75	150.88	28.99	62.31	133.64	120.78	125.57	59.21	117.26	77.52	99.48		

Table 2: Summary of the descriptive statistics for the physico-chemical environmental variables determined at all sites during the study period January to December 2015. The column shaded in light blue contains the overall descriptive statistics for the Mooi River (values of tributaries excluded in calculation). The columns containing the descriptive statistics of the tributaries (WFS, GM and WS) are shaded in purple. The Resource Quality Objectives (RQO) and Resource Water Quality Objectives (RWQO) set of numerical limits for the different variables are listed in the last two columns. Values exceeding both limits are highlighted in red, and values exceeding one limit, but not the other are highlighted in yellow. Values lower than both limits are highlighted in green. SD = Standard Deviation. - = No limits or data for the particular variable (continued)

Variables, abbreviations and unit	Descriptive	Mooi River	Site 1	WFS	Site 2	GM	Site 3	Site 4	WS	Site 5	Site 6	Site 7	Site 8	RQO limit	RWQO limit
Electrical Conductivity (EC) mS/m	Valid N	96	12	12	12	12	12	12	12	12	12	12	12		
	Mean	70.07	45.64	78.07	71.34	76.59	66.11	70.05	60.84	71.27	71.81	81.64	82.69	≤ 111	57
	Minimum	38.77	38.77	66.71	59.35	66.16	59.32	60.08	48.81	57.84	58.29	66.02	67.95		
	Maximum	109.90	56.30	96.96	86.69	93.80	84.18	95.47	79.61	93.63	104.20	108.20	109.90		
	SD	14.24	4.29	7.89	6.65	6.96	6.88	10.58	9.42	9.84	11.59	12.00	12.65		
Calcium (Ca^{2+}) mg/l	Valid N	96	12	12	12	12	12	12	-	12	12	12	12		
	Mean	70.06	58.93	87.73	73.20	69.60	62.80	56.63	-	80.67	74.53	77.20	76.53	-	47
	Minimum	9.20	24.00	52.80	38.40	19.20	36.80	9.20	-	48.00	51.20	59.20	54.40		
	Maximum	126.40	115.20	116.80	110.40	134.40	94.40	92.80	-	126.40	110.40	108.80	115.20		
	SD	21.81	23.82	19.53	22.23	28.82	17.58	22.77	-	24.86	21.51	14.38	16.94		
Magnesium (Mg^{2+}) mg/l	Valid N	96	12	12	12	12	12	12	-	12	12	12	12		
	Mean	48.90	37.74	43.84	49.70	54.74	49.93	51.49	-	48.39	50.90	48.58	54.49	≤ 33	30
	Minimum	8.80	8.80	28.30	28.30	17.60	26.40	20.50	-	26.40	27.30	30.30	31.20		
	Maximum	101.50	76.10	63.40	78.10	105.40	68.30	70.30	-	65.40	84.90	75.20	101.50		
	SD	15.18	17.49	10.73	15.00	20.33	11.21	14.26	-	14.23	17.44	11.75	17.35		
Chloride (Cl^-) mg/l	Valid N	96	12	12	12	12	12	12	-	12	12	12	12		
	Mean	46.25	13.58	42.42	36.50	46.67	39.25	43.42	-	48.17	46.58	69.83	72.67	-	36
	Minimum	5.00	5.00	35.00	25.00	41.00	32.00	32.00	-	34.00	33.00	32.00	55.00		
	Maximum	116.00	45.00	50.00	47.00	52.00	50.00	75.00	-	67.00	65.00	116.00	113.00		
	SD	21.98	10.63	4.21	5.57	2.96	4.99	12.63	-	8.39	8.77	24.90	19.36		
Fluoride (F^-) mg/l	Valid N	96	12	12	12	12	12	12	-	12	12	12	12		
	Mean	0.39	0.25	0.23	0.27	0.34	0.23	0.36	-	0.62	0.63	0.35	0.42	≤ 3	0.25
	Minimum	0.01	0.02	0.00	0.01	0.06	0.01	0.03	-	0.06	0.05	0.17	0.18		

Table 2: Summary of the descriptive statistics for the physico-chemical environmental variables determined at all sites during the study period January to December 2015. The column shaded in light blue contains the overall descriptive statistics for the Mooi River (values of tributaries excluded in calculation). The columns containing the descriptive statistics of the tributaries (WFS, GM and WS) are shaded in purple. The Resource Quality Objectives (RQO) and Resource Water Quality Objectives (RWQO) set of numerical limits for the different variables are listed in the last two columns. Values exceeding both limits are highlighted in red, and values exceeding one limit, but not the other are highlighted in yellow. Values lower than both limits are highlighted in green. SD = Standard Deviation. - = No limits or data for the particular variable (continued)

Variables, abbreviations and unit	Descriptive	Mooi River	Site 1	WFS	Site 2	GM	Site 3	Site 4	WS	Site 5	Site 6	Site 7	Site 8	RQO limit	RWQO limit
Fluoride (F^-) mg/l (continued)	Maximum	2.19	0.55	0.41	0.55	0.59	0.48	1.26	-	2.19	1.95	0.81	0.72		
	SD	0.36	0.14	0.14	0.19	0.16	0.17	0.34	-	0.62	0.54	0.17	0.17		
Sulfate (SO_4^{2-}) mg/l	Valid N	96	12	12	12	12	12	12	12	12	12	12	12		
	Mean	115.58	27.00	143.67	112.00	158.67	119.33	125.00	70.33	136.33	137.33	139.00	128.67	≤ 500	75
	Minimum	12.00	12.00	84.00	80.00	96.00	72.00	72.00	36.00	60.00	100.00	84.00	84.00		
	Maximum	220.00	56.00	252.00	136.00	344.00	172.00	216.00	156.00	204.00	220.00	196.00	208.00		
	SD	45.51	13.97	43.00	17.97	63.30	27.65	36.63	43.30	37.77	34.47	30.56	35.48		
pH	Valid N	96	12	12	12	12	12	12	12	12	12	12	12		
	Mean	8.18	8.16	8.17	8.07	8.11	8.37	8.25	8.50	8.16	8.18	8.10	8.14	≤ 8.8	8
	Minimum	7.50	7.66	7.55	7.68	7.60	7.84	7.50	7.48	7.69	7.74	7.64	7.82		
	Maximum	9.16	9.06	9.02	8.86	8.87	9.16	9.06	9.38	8.75	8.70	8.57	8.85		
	SD	0.35	0.42	0.42	0.37	0.37	0.39	0.43	0.58	0.29	0.29	0.32	0.27		
Turbidity NTU	Valid N	96	12	12	12	12	12	12	11	12	12	12	12		
	Mean	3.77	1.06	2.59	2.22	0.59	2.57	3.48	23.71	3.63	6.08	4.86	6.23	-	-
	Minimum	0.21	0.23	0.44	0.26	0.14	0.25	0.26	6.97	0.21	0.57	0.55	0.96		
	Maximum	18.30	1.73	6.57	5.34	0.89	5.15	7.45	118.00	10.40	14.90	18.30	16.20		
	SD	3.79	0.49	1.81	1.65	0.26	1.46	2.44	31.87	3.26	4.45	4.79	5.81		

Table 3: List of phytoplankton phyla and genera, with authorities, identified at each site. Mooi River sites are arranged in white shaded columns, and arranged from the upstream to the downstream sites. Tributaries (WFS, GM, and WS) are shaded in grey and are arranged according to their position of convergence with the Mooi River. Black crosses indicate the presence of genera at each site, while red crosses indicate dominant genera or genera found in high numbers. * = Genera previously classified under the phylum Chlorophyta (John et al. 2002), but currently classified under the phylum Charophyta according to Algaebase (Guiry & Guiry, 2019)

GENUS AND AUTHOR	UBD	WFS	BDI	GM	BDC	PD	WS	RB	SB	DFE	Krom
PHYLUM CYANOPHYTA (cyanobacteria/ blue-green bacteria)											
Anabaena Bory ex Bornet et Flahault	X	❌			X	X	❌	X	X		X
Aphanocapsa Nägeli	X	X	X		X	X	X	X		X	X
Aphanothece Nägeli					X	X					
Arthrospira Stizenberger ex Gomont							X				
Chroococcus Nägeli							X				
Merismopedia Meyen	X	X	X		X	X	❌		X	X	❌
Microcystis Kützing ex Lemmermann		❌	❌	❌	X	X	❌	❌			
Nostoc Vaucher ex Bornet & Flahault	X										
Oscillatoria Vaucher ex Gomont		X			X	X				X	X
Phormidium Kützing ex Gomont			X	❌	X	X	X	X	X	X	
Pseudanabaena Lauterborn	X	X	X	X	X	X	X	X	X	X	X
Spirulina Turpin ex Gomont		❌	X			X	X				
Synechocystis Sauvageau		X	X		X	X	X	X	X	X	
Unknown round colonies		X		X							
Total Cyanophyta genera	**5**	**9**	**7**	**4**	**9**	**10**	**10**	**6**	**5**	**6**	**5**
PHYLUM BACILLARIOPHYTA (diatoms)											
Achnanthidium Kützing	X	X	X	X	X	X	X	X	X	X	X
Amphora Ehrenberg ex Kützing					X				X	X	
Aulacoseira Thwaites	X	❌	❌	X	X	X	X	❌	❌	X	X
Cocconeis Ehrenberg	X	X	X	X	X	X	X	X	X	X	❌
Craticula Grunow		X	X	X		X		X	X		
Cyclotella Kützing ex Brébisson	❌	❌	❌	❌	X	X	X	❌	❌	❌	X
Cymatopleura Smith		X					X	X	X		X
Cymbella Agardh	X	X	X	X	X	X		X	X		X
Diadesmis Kützing	X		X	X	X	X		X	X	X	X
Diatoma Bory	X	X		X	X	X	X	❌	❌		X

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GENUS AND AUTHOR	UBD	WFS	BDI	GM	BDC	PD	WS	RB	SB	DFE	Krom
PHYLUM BACILLARIOPHYTA (diatoms) (continued)											
Encyonema Kützing		X	X		X	X					
Epithemia Kützing				X		X					
Fragilaria Lyngbye	X	X	X	X	X	X	X	X	X	X	X
Frustulia Agardh										X	
Gomphonema Ehrenberg	X	X	X	X	X	X	X	X	X	X	X
Gyrosigma Hassall							X	X		X	X
Hantzschia Grunow				X	X	X		X	X	X	X
Hippodonta Lange-Bertalot, Witkowski & Metzeltin							X				
Melosira Agardh		X		X	X	X		X	X		X
Navicula Bory	X	X	X	X	X	X	X	X	X	X	X
Nitzschia Hassall	X	X	X	X	X	X	X	X	X	X	X
Pinnularia Ehrenberg	X	X		X	X	X	X	X		X	X
Placoneis Mereschkowsky	X										
Pleurosigma Smith									X		
Rhoicosphenia Grunow	X	X	X	X	X	X	X	X	X	X	X
Sellaphora Mereschowsky		X		X	X	X		X	X		
Staurosira Ehrenberg		X	X	X	X	X	X	X	X	X	X
Surirella Turpin	X	X		X	X	X	X		X		X
Tabellaria Ehrenberg ex Kützing		X		X					X	X	X
Tryblionella Smith	X					X		X	X		X
Unidentified pennate diatom	X	X	X	X	X	X	X	X	X	X	X
Total Bacillariophyta genera	16	20	14	**21**	**20**	**22**	**16**	**21**	**23**	**17**	**21**
PHYLUM CHLOROPHYTA (green algae)											
Ankistrodesmus Corda	X	X	X		X	X	X			X	X
Carteria Diesing	X		X		X	X		X		X	X
Chlamydomonas Ehrenberg	X	X	X	X	X	X	X	X	X	X	X

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GENUS AND AUTHOR	UBD	WFS	BDI	GM	BDC	PD	WS	RB	SB	DFE	Krom
PHYLUM CHLOROPHYTA (green algae) (continued)											
Chlorella Beijerinck	X	X	X	X	X	X	X	X	X	X	X
Chlorococcum Meneghini	X	X	X	X	X	X	X	X	X	X	
Chlorolobion Korshikov	X										
**Closterium* Nitzsch ex Ralfs	X	X	X	X	X	X	X	X	X	X	X
Coelastrum Nägeli	X		X	X	X	X	X	X	X	X	
**Cosmarium* Corda ex Ralfs		X	X	X	X	X	X		X	X	
Crucigenia Morren	X	X	X		X	X		X	X	X	X
Crucigeniella Lemmerman	X		X		X	X	X	X	X	X	X
Desmodesmus An, Friedl & Hegewald	X	X	X	X	X	X	X	X	X	X	X
Dictyosphaerium Nägel	X		X		X	X	X		X		X
Eudorina Ehrenberg ex Ralfs							X			X	
Geminella Turpin			X		X	X		X			
**Gonatozygon* De Bary				X							
Kirchneriella Scmidle							X			X	
Microspora Thuret	X										
Monoraphidium Komárková-Legnerová	X	X	X	X	X	X	X	X	X	X	X
**Mougeotia* Agardh	X	X	X	X				X	X	X	
Oocystis Braun	X	X	X	X	X	X	X	X	X	X	X
Pandorina Bory de Saint-Vincent							X				
Pediastrum Meyen		X	X		X	X	X	X	X	X	X
Scenedesmus Meyen	X	X	X	X	X	X	X	X	X	X	X
Schroederia Lemmermann	X			X	X	X	X	X	X	X	
Sphaerocystis Chodat		X	X	X	X	X					
**Staurastrum* Meyen ex Ralfs	X		X	X	X	X	X				
Tetraedron Kützing	X	X	X	X	X	X	X	X	X	X	X
Tetrastrum Chodat	X			X	X	X	X	X			X

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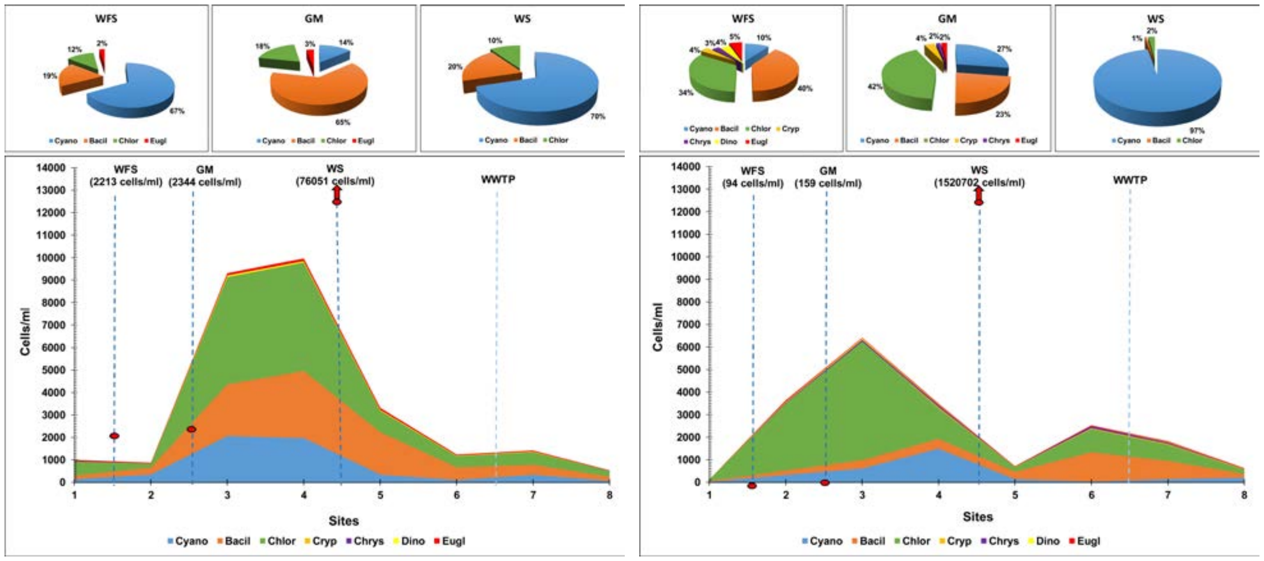
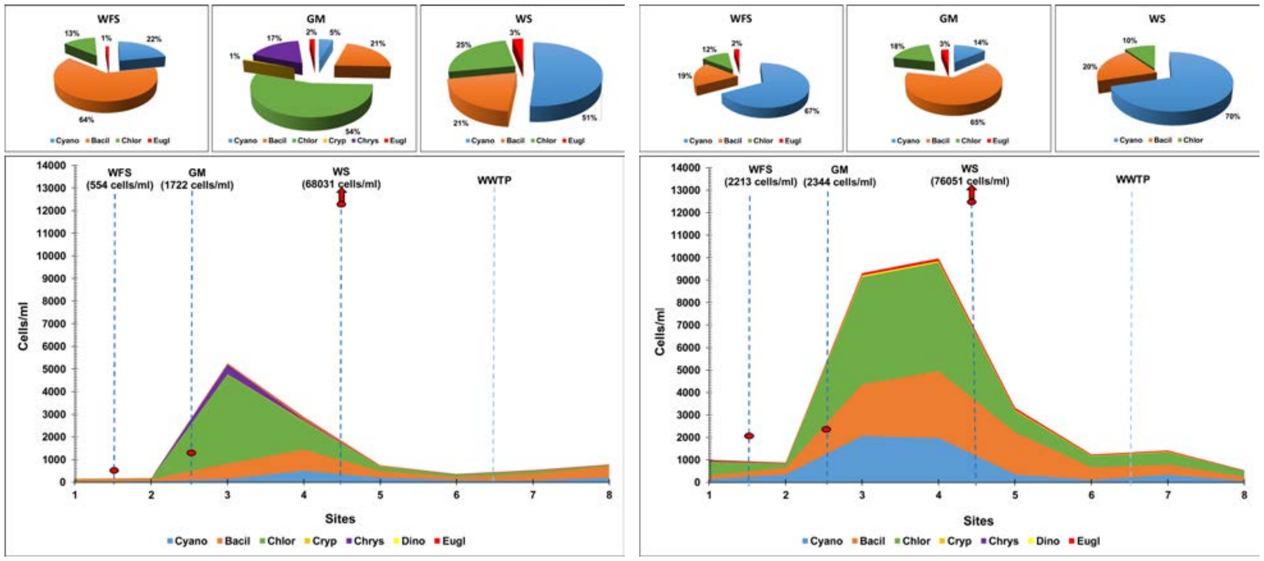
GENUS AND AUTHOR	UBD	WFS	BDI	GM	BDC	PD	WS	RB	SB	DFE	Krom
PHYLUM CHLOROPHYTA (green algae) (continued)											
Treubaria Bernard emend. Reymond	X				X	X			X	X	X
Ulothrix Kützing					X	X		X	X	X	X
Total Chlorophyta genera	**22**	**15**	**21**	**17**	**25**	**24**	**21**	**19**	**19**	**22**	**17**
PHYLUM CRYPTOPHYTA (cryptophytes)											
Cryptomonas Ehrenberg	X	X	X	X	X	X	X	X	X	X	X
Total Cryptophyta genera	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
PHYLUM CHRYSOPHYTA (golden-brown algae)											
Dinobryon Ehrenberg	X	X	X	X	X	X	X	X	X	X	X
Synura sp. Ehrenberg								X		X	X
Total Chrysophyta genera	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**1**	**2**	**2**
PHYLUM DINOPHYTA (dinoflagellates)											
Ceratium Schrank	X	X		X	X	X	X	X		X	
Peridinium Ehrenberg	X		X		X	X	X	X	X	X	X
Sphaerodinium Woloszynska		X	X	X		X		X			
Total Dinophyta genera	**2**	**2**	**2**	**2**	**2**	**3**	**2**	**3**	**1**	**2**	**1**
PHYLUM EUGLENOPHYTA (euglenoids)											
Euglena Ehrenberg	X	X	X	X	X	X	X	X	X	X	X
Lepocinclis Perty				X	X	X			X	X	X
Phacus Dujardin							X	X		X	X
Strombomonas Deflandre		X		X			X				
Trachelomonas Ehrenberg	X	X	X	X	X	X	X	X	X	X	X
Total Euglenophyta genera	2	3	2	4	3	3	4	3	3	4	4
TOTAL NUMBER OF GENERA PER SITE	**49**	**51**	**48**	**50**	**60**	**64**	**55**	**55**	**53**	**54**	**51**



A: Summer

B: Autumn



C: Winter

D: Spring

Figure 2: Cumulative phytoplankton density (cells/ml) and diversity in the Mooi River during 2015. Dark blue vertical dotted lines indicate inflows of the WFS, GM and the WS, while the light blue vertical dotted line indicates the location of the WWTP. The phytoplankton diversity in each tributary is illustrated with a pie chart. Red dots represent the mean phytoplankton density (cells/ml) for the WFS, GM, and WS, while the total phytoplankton density is given in brackets. Red arrows represent values exceeding values on the Y-axis. Cyano = Cyanophyta, Bacil = Bacillariophyta, Chlor = Chlorophyta, Cryp = Cryptophyta, Chrys = Chrysophyta, Dino = Dinophyta, and Eugl = Euglenophyta.

Figure 2A–D illustrates phytoplankton density and diversity at different sites in the Mooi River. Pie charts illustrate phytoplankton diversity in the three tributaries for the same time periods. During the entire study period a mixture of Chlorophyta, Bacillariophyta and Cyanophyta was found in the Mooi River main stream. These three phyla also dominated in the tributaries, where small percentages of other algal phyla were noticeable. Phytoplankton reached highest densities during summer months (Figure 2A), whereafter the density decreased through autumn (Figure 2B) to the winter period (Figure 2C). With the onset of spring (Figure 2D), the general phytoplankton density increased again towards summer.

When phytoplankton density in the tributaries was compared to that in the Mooi River, it was clear that the densities in the WFS and GM were low. However, phytoplankton density in the WS was much higher than at any site in the Mooi River. Besides Chlorophyta, Bacillariophyta and Cyanophyta, relatively small percentages of Euglenophyta were found across seasons in most tributaries (Figure 2A–D). In winter (Figure 2C), high densities of *Dinobryon,* a colonial member of the Chrysophyta, was responsible for a 17% contribution of Chrysophyta to the total phytoplankton diversity in GM. *Dinobryon* was also present in high densities at Site 3 in the Mooi River during winter. In contrast to all sites in

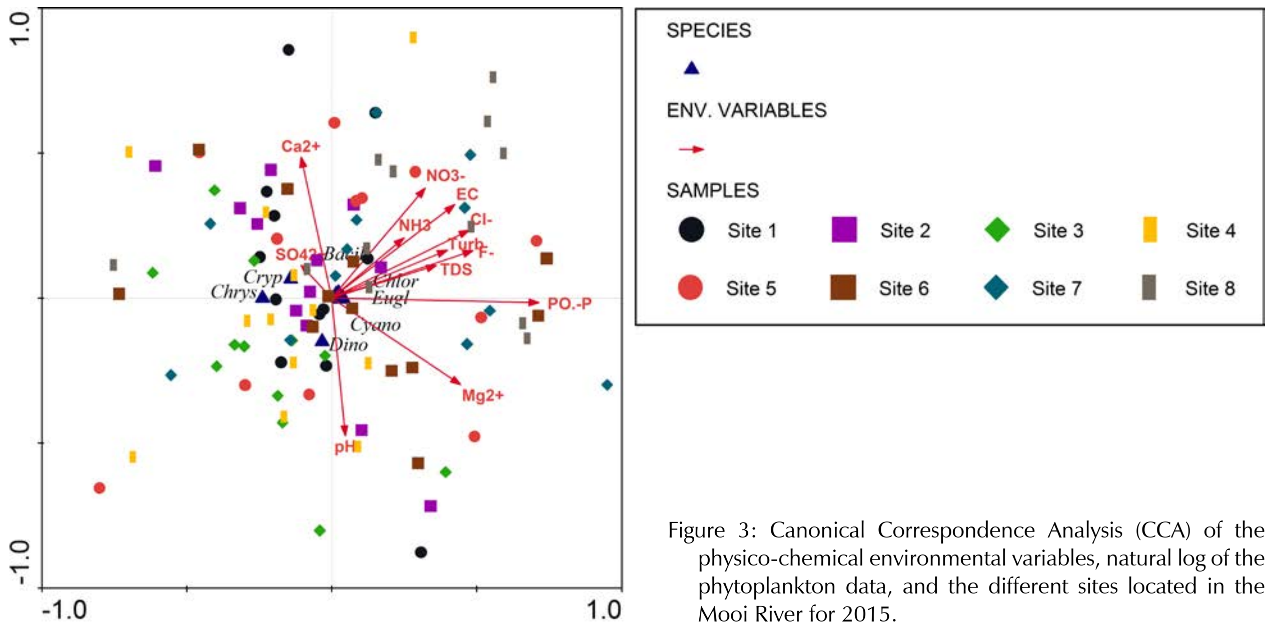


Figure 3: Canonical Correspondence Analysis (CCA) of the physico-chemical environmental variables, natural log of the phytoplankton data, and the different sites located in the Mooi River for 2015.

the Mooi River, WFS and GM, the WS was dominated by cyanobacteria during all seasons. During summer and autumn, cyanobacteria in the WSD comprised 70% and 97% of the total phytoplankton, respectively. During the summer months common cyanobacteria in the WS included *Anabaena*, *Merismopedia* and *Microcystis,* while the dominance of cyanobacteria during autumn in the WS could be ascribed exclusively to a bloom of *Microcystis*. Cyanobacteria, such as *Anabaena* and *Microcystis,* also dominated during summer months in the WFS (67%; Figure 2A). During autumn (Figure 2B) the WFS was diverse in terms of the number of phyla present.

Noticeable patterns were observed regarding spatial distributions of phytoplankton in the Mooi River. In general, densities were low at the uppermost sites (1 and 2) of the river. Downstream from the Boskop Dam, an increase in phytoplankton density was observed across all seasons. Maximum densities were recorded at Site 3 (in autumn, winter and spring) and Site 4 (summer). From Site 3 the phytoplankton density showed a general downstream decrease to the confluence of the Mooi and the Vaal rivers. It does not seem as if the inflow of the WS, with high phytoplankton densities (especially cyanobacteria), had a marked effect on phytoplankton density or diversity in the Mooi River's main stream downstream from the inflow.

Results of a multivariate analysis, in the form of a CCA performed on physico-chemical and phytoplankton data at the different sites, are presented in Figure 3. The CCA only includes data from the Mooi River and not the tributaries as the purpose of the CCA was to draw a conclusion for conditions in the river itself, and to see how different water quality variables relate to one another in the main stream.

Eigenvalues for the first four axes of the CCA are presented in Table 4. The first axis explained 58% of the variance in the species–environmental data, while the second axis explained an additional 25% of the variance in the species–environment relationship. The Monte Carlo Permutation test on all canonical axes (number of permutations = 499) showed a P-value of 0.006 and an F-ratio of 1.767, indicating that the environmental (physico-chemical) variables significantly correlated with the phytoplankton data. The CCA confirms significant relationships between variables. EC, TDS, and turbidity had strong positive correlations with one another, as well as with chloride (Cl^-) and fluoride (F^-).

As a result of inflation, TDS was eliminated from the CCA (Figure 4) and EC was used as a representative of salinity. The statistical significance of this correlation was supported by Kruskal-Wallis correlation values of $P < 0.05$. Calcium (Ca^{2+}) and Magnesium (Mg^{2+}), in contrast, showed a statistical significant ($P < 0.05$) negative correlation with each other as their vectors point in opposite directions (Figure 3). Cyanobacteria (Cyano) was positively correlated with orthophosphate (PO_4-P), pH and magnesium (Mg^{2+}).

The length of the orthophosphate vector indicates that it was the most important variable having the most influence on the axis. The positive correlation between cyanobacteria and orthophosphates, coupled with orthophosphates having the most important influence, emphasise the importance of orthophosphate on cyanobacteria dynamics. Besides orthophosphates, cyanobacteria also showed positive correlations with nutrients, such as ammonia (NH_3^+) and nitrates (NO_3^-). Chlorophyta, Bacillariophyta and Euglenophyta were also correlated positively with nutrient concentrations. Cryptophyta, Chrysophyta and Dinophyta that did not

Table 4: Eigenvalues of the CCA on the phytoplankton and physico-chemical variable data of the Mooi River from January to December 2015

	Axes				
	1	2	3	4	**Total**
Eigenvalues	0.032	0.014	0.006	0.002	0.291
Species–environment correlations	0.484	0.437	0.398	0.297	
Cumulative percentage variance of species data	11.0	15.7	17.9	18.5	
Cumulative percentage variance of species–environment relation	58.3	83.4	95.2	98.3	
Sum of Eigenvalues					0.291
Sum of all canonical eigenvalues					0.055

occur frequently or in high density, were generally associated with low phosphate concentrations, as well as low EC and turbidity values. pH was negatively correlated with most physico-chemical variables, except magnesium. Site 3 and Potchefstroom Dam, displayed the highest phytoplankton density recorded for the Mooi River, and these sites were negatively correlated with nutrients.

Discussion

Physico-chemical variables

The National Water Act, Act No. 36 of 1998, uses different sets of scientific criteria, one of which focuses on the physico-chemical variables. These criteria are abbreviated as RQO (see results for full names). Limits set by the criteria can be seen as goals to strive for, in order to achieve a certain desired water quality for a specific area. The notion is to compare these limits to current findings to determine if they are met (Dickens, Pringle & Macfarlane 2011). RQO play an important role in water resource management because it is easier to have clear sets of criteria to work towards and in this way the protection of water becomes a reality (Dickens et al. 2011). Nine water management areas (WMA's) were identified in South Africa (DWS 2016) and the RQO criteria differ for each WMA. The Mooi River is classified under the Vaal WMA for which the RQO are currently under review (Labuschagne 2017); however Dickens et al. (2011) proposed that available information should be used, where possible. A second set of criteria, RWQO, that specifically target the Mooi River catchment, was recommended by The Department of Water Affairs (DWA 2009). Concentration ranges of physico-chemical variables were examined and compared with existing RQO and RWQO (Table 2).

In general, nutrient concentrations measured in the Mooi River, as well as in all three tributaries, were high and mean values usually exceeded limits set by both RQO and RWQO (Table 2). An exception was the orthophosphate concentration in WFS and at two sites in the main stream that exceeded the RQO limit, but still fell within RWQO limit. It is well known that anthropogenic activities result in elevated nutrient levels that can ultimately lead to eutrophication of a water body. According to Fu et al. (2012) the main causes of elevated ammonia levels are urban, agricultural (especially pig and poultry farming), and industrial runoff. The highest mean and maximum ammonia concentrations in the main stream of the Mooi River were measured at sites 5 and 6, located just downstream from the inflow of the WS (Table 2). A sudden elevation in ammonia levels at these two sites (Figure 1) can be ascribed to inflow of ammonia from the WS (mean ammonia of 1.12 mg/l). The WS flows through the industrial area of Potchefstroom where it receives several point sources of pollution. Urban and storm water effluents further downstream also contribute to high ammonia levels. Other factors that may contribute to high ammonia concentrations in the Mooi River include pig farming in the upper reaches, WWTP's in the catchment of tributaries and peat mining.

According to Bourbonniere (2009), peat mining drainage results in elevated ammonia concentrations in water bodies through decomposition of soil. Irrigation, agriculture and sewage effluents are known to elevate nitrate concentrations in water bodies (Tredoux, Engelbrecht & Israel 2009). All these land uses are common practices in the catchment of the Mooi River and may have resulted in nitrate concentrations exceeding the RWQO limit. Highest mean and maximum nitrate concentrations were found at Site 1 in the Mooi River, the middle reaches (sites 4 and 5), and also downstream from the WWTP (Site 7). Unfortunately, no samples were taken from the WWTP. At the uppermost site in the river (Site 1) intensive agricultural activities, coupled with irrigation, may have resulted in elevated nitrate levels, while effluents from the WS (mean nitrate concentration of 1.12 mg/l) and WWTP may have resulted in high nitrate concentrations at sites 5 and 7, respectively. When the sum of ammonia and nitrate in the Mooi River and its tributaries is compared to the dissolved inorganic nitrogen ranges in Department of Water Affairs & Forestry (DWAF 1996e) and Dallas and Day (2004), it is clear that the Mooi River system can be classified as mesotrophic in terms of inorganic nitrogen concentration.

Mean orthophosphate concentrations in the entire Mooi River, the GM and the WS exceeded both guidelines. The mean concentration in the WFS (0.34 mg/l) exceeded the RQO limit of ≤ 0.125 mg/l but was within the limit of 0.4 mg/l set by the RWQO (Table 2). Highest orthophosphate concentrations were recorded at Site 7 (Figure 1) located just downstream from the WWTP. It is, however, suspected that return flows from the treatment plant may have been rich in orthophosphates and it is therefore recommended that sampling sites before and after the inflow of the WWTP should be included in future research. Muscutt and Withers (1996) found that orthophosphates are mainly influenced by agricultural, industrial and sewage effluents, all pronounced activities in the Mooi River's catchment. Mean orthophosphate concentrations in the tributaries ranged from 0.34 mg/l (WFS) to 0.54 mg/l (GM) to 1.02 mg/l (WS). The inflow of WS was responsible for doubling the mean orthophosphate concentration from 0.36 mg/l (site 4) to 0.72 mg/l (site 5; Table 2). According to DWAF, 1996e), orthophosphate concentrations above 0.25 mg/l are indicative of hypertrophy. Based on mean values for the entire Mooi River, and the tributaries, the Mooi River system can be classified as hypertrophic in terms of orthophosphate concentration.

TDS and EC are usually positively correlated with each other as both variables provide an indication of salinity caused by major ions and electrically charged particles in the water. The RWQO limit for TDS in the Mooi River is 370.5 mg/l, while that of EC is 57 mS/m. TDS and EC at Site 1 of the Mooi River did not exceed these limits. Mean TDS concentrations exceeded the RWQO limit at sites further downstream. Mean EC downstream of Site 1 also exceeded the RWQO guideline, but still fell within the RQO limit. The salinity of most inland waters is usually between 100 and 500 mg/l (Wetzel 2001). Salinity (TDS) in the Mooi River and its tributaries exceeded 400 mg/l. Although TDS concentration at Site 1 of the Mooi River falls within the RWQO guideline, it is still more than double the 100 mg/l found in most rivers worldwide. High TDS/EC in the Mooi River can be ascribed to the dolomitic geology underlying the area, irrigation along the length of the river, leaching and erosion from older tailings storage facilities (Van der Walt et al. 2002), as well as several point sources of pollution e.g. various waste water effluents from dewatering mines and WWTP's, industrial effluents, and poorly treated sewage effluents from informal settlements. The highest mean TDS concentration of approximately 560 mg/l was found in the GM tributary and the site located just downstream of the WWTP (Site 7). Maximum and highest mean EC was found at the two most downstream sites in the river. It therefore seems as if return flows from the WWTP could have contributed to both elevated TDS and EC levels, as well as increasing nutrient concentrations in the downstream section of the Mooi River.

A high rate of abstraction for irrigation also dramatically reduces the flow rate in this section of the river. TDS is the sum of major ions, and therefore relates positively with cations (calcium, magnesium, sodium, and potassium) and anions (bicarbonate, carbonate, chloride, sulfate, and fluoride). Sulfate was the most abundant major ion in the Mooi River system (Table 2). Sulfate pollution is known to be caused by mining activities (Durandt 2012), explaining maximum sulfate concentrations in the WFS and GM tributaries, which are surrounded by mines. Sulfate concentrations in GM, where peatlands are found (Figure 1), exceeded that of WFS (Table 2). According to Coleman Wasik et al. (2015), peatlands are considered to be sinks for atmospherically deposited sulfate and, coupled with droughts, may further elevate sulfate concentrations in aquatic environments. Sulfate, chloride and fluoride concentrations fell within the RWQO limits at the uppermost site of the river, however as the river continued its path downstream all these concentrations increased and the mean concentration of the entire Mooi River exceeded the RWQO goal. Mean calcium and magnesium concentrations exceeded goals set by the RWQO at all sites.

The mean pH in Mooi River and all the tributaries slightly exceeded the RWQO limit of 8, but not the RQO limit of ≤ 8.8 (Table 2). Generally, mean pH ranges between 6 and 8.9 in fresh waters (Dallas & Day 2004). Mean pH values for the entire Mooi River and the tributaries corresponded to these ranges. If pH exceeds 8, ammonium is converted to ammonia, which is potentially toxic to aquatic organisms (Dallas & Day 2004). High pH levels in the WS may explain high ammonia concentrations at this site (Table 2). High phytoplankton densities in the WS (Figure 2) could have elevated the pH as a result of the uptake of CO_2 during photosynthesis.

Turbidity was the lowest at Site 1 and the highest at the most downstream site (Site 8) in the Mooi River. Turbidity is the result of inorganic and organic suspended solids (Dallas & Day 2004), and dependent on the flow rate of the water bringing particles into suspension. At Site 8, a weir is built in the river, that resulted in high flow rates and fast mixing that keeps particles in suspension. Water in the GM (a spring) was extremely clear (mean turbidity of 0.59 NTU), while the mean turbidity in the WS (24 NTU) was the highest measured in the Mooi River system. High turbidity levels in the WS can be ascribed to high phytoplankton densities reaching more than 1.5 million cells/ml at times

(Figure 2B). No RQO or RWQO guidelines were set for turbidity; however guidelines were presented in the DWAF (1996a–d) water quality guidelines for water for domestic, recreational, agricultural and industrial use. These guidelines do, however, differ considerably for the type of water usage. In general, turbidity levels in the tributaries did not influence turbidity in the Mooi River system significantly, probably as a result of dilution. It is possible that the flow in the Mooi River far exceeded that in the tributaries, but actual flow data would be required to test this.

Phytoplankton density and diversity

River systems are often dominated by Bacillariophyta, Chlorophyta and Cyanophyta and succession between these three phyla as the dominants, as was found in the Mooi River, is well known from literature on rivers throughout the world (Sarwade & Kamble 2013). Of these three phyla, Cyanophyta is potentially problematic and blooms can result in, amongst others, aesthetically unacceptable scum formations, recreational problems, such as skin and eye irritations, and the production of tastes, odours and toxins (Mankiewicz et al. 2003).

In general, low phytoplankton densities were recorded at Site 1. As the Mooi River originates from an eye (spring), it can be reasoned that low phytoplankton densities can be ascribed to pristine, oligotrophic spring water, containing low nutrient concentrations. However, nutrient concentrations at the uppermost site (Site 1) of the river were comparable to concentrations further downstream, where phytoplankton was found in high densities. Elevated nutrient concentrations at Site 1 can be the result of agricultural activities in the surrounding area. Low turbidity levels at Site 1 allowed for sufficient photosynthetically available radiation. However, overhanging riparian vegetation could have blocked light penetration, which can explain lower phytoplankton densities. Site 1 is also located far upstream close to the origin of the river, resulting in limited time for phytoplankton establishment. Other factors such as flow rate and water temperature have an influence on phytoplankton growth (Falkowski, Greene & Geider 1992), but were not measured.

Chlamydomonas, indicative of organic pollution (Bellinger & Sigee 2010), was found in high densities at Site 1. Other potential problematic algae encountered at this site included *Cyclotella,* reported to produce taste and odour problems (Bellinger & Sigee 2010; Palmer 1969). *Nostoc* is a nitrogen-fixing cyanobacterium associated with nitrogen-deficient habitats (Douterelo, Perona & Mateo 2004). Several studies on river systems found *Nostoc* to be dense at upstream sites while absent downstream, which was ascribed to low nutrient concentrations upstream (Douterelo et al. 2004; Janse van Vuuren & Taylor 2015). This was, however, not the case for Site 1 with moderate nutrient concentrations. Some *Nostoc* species are able to produce toxins in fresh waters (Bellinger & Sigee 2010). *Chlorolobion*, *Placoneis* and *Microspora* were present in low concentrations exclusively at the uppermost site of the Mooi River (Table 3). *Placoneis* can be present in a broad range of water chemistry (unpolluted water, slightly polluted water, brackish water, and sediments; Taylor et al. 2007). *Microspora* often dominates in streams contaminated with heavy metals (John et al. 2002) and its presence at the uppermost site of the Mooi River can be the result of heavy metal pollution by mines in WFS and GM areas (via underground compartments – data on heavy metals not presented).

Results in Figure 2 show that maximum phytoplankton density during all seasons was found in the middle reaches of the Mooi River (sites 3 and 4), located between Boskop Dam and the city of Potchefstroom. Sites 3 and 4 reflected very similar water quality conditions (Table 2), with nutrient levels high enough to sustain phytoplankton growth. Agricultural activities and an ammunition manufacturing company are the only known factors that may have contributed to water pollution at sites 3 and 4 (Table 1). Sufficient nutrients, coupled with relatively low turbidity levels, could have stimulated phytoplankton growth in the middle reaches. Nutrient spiralling from upstream may have provided an important nutrient source. High phytoplankton densities at these sites could result in higher mean pH values compared to other sites in the Mooi River's main stream (Table 2). In general, phytoplankton at these sites consisted of a mixture of Chlorophyta, Bacillariophyta and Cyanophyta, with a relatively small percentage of Chrysophyta (*Dinobryon*) during winter. *Dinobryon* was probably introduced into the main stream by GM in which it comprised 17% of the total phytoplankton diversity (Figure 2).

Cyanobacteria reached maximum densities in the middle reaches of the river and their presence was associated with water quality problems. Genera that were most dense in sites 3 and 4 included: *Anabaena*, *Aulacoseira*, *Cyclotella*, *Diatoma*, *Geminella*, and *Ulothrix* (Table 3). Taylor et al. (2007) stated that *Diatoma* is indicative of hard water, coupled with high nutrient levels, corresponding to conditions found at sites 3 and 4 (Table 2). *Diatoma* occurs in rivers and slow flowing waterbodies, where they usually attach to green algae, and high *Diatoma* densities correspond to high densities of Chlorophyta present at sites 3 and 4 (Figure 2). High numbers of *Aulacoseira* in sites 3 and 4 corresponded to the findings of Luyt (2018) and can most probably be attributed to high EC levels. Both *Aulacoseira* and *Cyclotella* can cause taste and odours, as well as significant filter clogging problems during drinking water purification (Bellinger & Sigee 2010; Palmer 1969).

Downstream sites (sites 5 to 8) in the Mooi River had low phytoplankton densities, comparable to densities found at the uppermost site. These sites displayed high turbidity levels, which could have limited photosynthetically available radiation. Large trees on the banks shading the river may also have contributed to less light penetrating the water. Fast flow rates at the weir at Site 8, probably suppressed the development of phytoplankton, resulting in low densities. High nutrient concentrations at sites 5 to 8 (Table 2) could have favoured the growth of *Aulacoseira, Coelastrum, Diatoma, Dictyosphaerium, Merismopedia, Microcystis, Pediastrum, Scenedesmus,* and *Ulothrix* as they are often associated with nutrient-enriched conditions (Bellinger & Sigee 2010). *Aulacoseira* prefers high EC levels (Luyt 2018), explaining their presence at sites 5 and 6 with high TDS concentration and EC levels (Table 2). *Diatoma* is typically found in the middle and lower reaches of the river that displayed hard water conditions (Table 2).

Phytoplankton density and diversity in the tributaries did not change the Mooi River's phytoplankton assemblages downstream of their inflows. Research in Brazil (Rodrigues et al. 2009) showed that medium and large tributaries are able to influence main rivers in terms of phytoplankton dynamics. Outcomes of the research for smaller tributaries, such as those found in the Mooi River catchment, differ (Bahnwart, Hubener & Schubert 1999). The WFS is a small tributary that is often dry, feeding the Mooi River only during high rainfall periods. The WFS did not have any apparent impact on phytoplankton density or diversity in the main stream after the inflow (Figure 2). Similar genera were observed in the GM and at sites downstream of its inflow. During winter *Dinobryon* (phylum Chrysophyta) was prominent in GM, and at the same period *Dinobryon* colonies were also present at site 3 located just downstream from the GM inflow (Figure 2C). It is uncertain whether similarities were due to importation of *Dinobryon* via the GM tributary, or whether it could be the result of other factors, such as nutrient concentrations or seasonality, because *Dinobryon* is known to prefer cold water conditions (Heinze et al. 2013).

The WS tributary is often polluted by sewage, due to blocked pumps, and was dominated by extremely high densities of cyanobacteria as a result of mean nutrient concentrations exceeding 1.0 mg/l. During the present study, blooms in WS were present throughout the year and *Microcystis* formed a thick blue-green scum on the water's surface. Other genera present in high densities in the WS included: *Anabaena*, *Coelastrum*, *Cymatopleura*, *Diatoma*, *Eudorina*, *Gomphonema*, *Merismopedia*, *Pandorina*, *Pediastrum*, and *Scenedesmus* (Table 3). All these genera are known to prefer nutrient-rich water (Bellinger & Sigee 2010). *Gomphonema* often occurs in sewage-enriched water (Janse van Vuuren et al. 2006). *Hipodonta* is typically found in eutrophic conditions and can tolerate critical pollution levels (Taylor et al. 2007) – it was present in the WS, but absent from all other sites.

In spite of high phytoplankton numbers, the inflow of the WS did not have an apparent effect on phytoplankton density at downstream sites. Water from the WS flows through different areas, including a wetland and concrete canal, before it reaches Site 5. The concrete canal serves as an illegal dumping site for garden refuse and plant material that often establishes and grows in the WS absorbing bio-available nutrients, therefore improving the water quality before it flows into the Mooi River. Flow rates also slow considerably in the final stretch of WS and the water is rather shallow before it reaches the Mooi River, thus planktonic organisms may settle or become entrained in detritus before entering the Mooi River.

Multivariate analyses

Nutrients determine the rate of primary production and phytoplankton biomass and they were positively correlated with Bacillariophyta, Chlorophyta, Cyanophyta and Euglenophyta (Figure 3). Of all the nutrients, orthophosphates were the most influential (length of vector) and can be regarded as the main nutrient determining phytoplankton density in this study. Orthophosphates were strongly positively correlated with cyanobacteria (Figure 3) and results of this study support those of other studies, such as Elser, Marzolf & Goldman (1990), that phosphates stimulate cyanobacterial growth. Green algae and diatoms were the most dense and diverse phyla in the Mooi River. Felisberto, Leandrini and Rodrigues (2011) found green algae benefit from increased phosphorus in the Corvo River, Brazil. Although cyanobacteria were less diverse, they were abundant, especially at sites 3 and 4 and in the WS tributary.

Sites 3 and 4 correlated negatively with nutrients (Figure 3), probably as a result of high phytoplankton densities depleting nutrients. Maximum pH was recorded in the WS followed by sites 3 and 4 (Table 2). Positive relationships between cyanobacteria and turbidity, and cyanobacteria and pH, can be the result of suspended cyanobacteria responsible for elevated turbidity levels and photosynthesis responsible for elevated pH levels. According to Chorus and Bartram (1999), cyanobacteria have a competitive advantage in turbid conditions because they are specially adapted to absorb green light and therefore can live in environments with lower light intensities. Cyanobacteria have phycobiliproteins, which enable them to absorb a green portion of light (during low light intensities) and turn it to red light, which is the colour of light required by chlorophyll. In some cases cyanobacteria blooms may be the result of high turbidity levels, while in other cases cyanobacterial blooms may cause the high turbidity. This could explain the positive correlation between cyanobacteria and turbidity (Figure 3).

Some cyanobacteria, such as *Microcystis* and *Anabaena*, have gas vacuoles giving them the ability to float and they can form large green scums on the surface that prevents light passing through the water column. Euglenophyta was one of the less conspicuous phyla encountered (2% relative density). Although present in low densities, euglenoids were more abundant than Cryptophyta, Chrysophyta or Dinophyta. Euglenophyta were positively correlated with nutrients, TDS/EC and turbidity (Figure 3). This is in accordance to descriptions in Janse van Vuuren et al. (2006), stating that most species within this phylum are known to occur in nutrient-rich habitats. On the contrary, Cryptophyta and Chrysophyta showed a negative correlation with orthophosphates and turbidity (Figure 3), that supports findings by Palmer (1980) that these phyla are generally associated with clean and unpolluted water.

Conclusions

The entire Mooi River catchment area is subjected to pollution as a result of various land use activities contributing to elevated nutrient concentrations.

It can be concluded that the WFS, GM and WS tributaries affected the concentrations of physico-chemical variables in the Mooi River downstream from their points of inflow. In terms of nutrient (especially ammonia) concentrations, it was clear that all three tributaries affected the Mooi River downstream from their points of inflow. WS and the WWTP had a significant effect in terms of contributing to elevated nitrate and orthophosphate levels. The mean ammonia and nitrate concentrations are indicative of mesotrophic conditions, while the mean orthophosphate concentration is indicative of hypertrophic conditions. High TDS concentrations and EC levels in the tributaries also affected the Mooi River downstream from the points of inflow. Although no TDS and EC data were available for the WWTP, it seems as if it had a significant influence on downstream sites in the Mooi River and therefore further research on the effects of the WWTP on the Mooi River is strongly recommended.

Of the seven phytoplankton phyla found, green algae, diatoms and cyanobacteria were most dense and diverse, while euglenoids, dinoflagellates, golden-brown algae, and cryptophytes were found in low densities and diversity. In general, phytoplankton density and diversity were relatively low in the upper and lower reaches of the Mooi River, compared to the middle reaches (sites 3 and 4). Maximum density of cyanobacteria were found in the middle reaches of the river and were usually associated with water quality problems. Most genera found at sites 3 and 4 were indicative of high nutrient concentrations.

The phytoplankton density and diversity in the tributaries did not have a significant effect on the Mooi River's phytoplankton downstream. Similar genera were however, on occasion, observed in a tributary and the site just downstream from its inflow. Most phytoplankton found in the Mooi River and tributaries could be responsible for nuisance conditions. *Microcystis* and *Anabaena* are known to cause taste and odour problems and secrete toxins. The WS was entirely dominated by cyanobacteria with *Microcystis* reaching bloom proportions and forming thick scums at this site. These blooms were accompanied by high nutrient concentrations, high turbidity levels and relatively high pH values.

Nutrients positively correlated with diatoms, green algae, cyanobacteria and euglenoids. Orthophosphates and cyanobacteria showed a strong positive correlation, emphasising the important effect of this nutrient on cyanobacterial densities. Relatively low density and diversity of Chrysophyta and Cryptophyta, phyla generally associated with clean and unpolluted water, emphasise the fact that the Mooi River and its tributaries can be regarded as a polluted system with a continuous deterioration in water quality over time.

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Authors' contributions

LK did the sampling and research as part of her MSc project and also wrote part of the text. SJvV assisted in phytoplankton identification, wrote the text and was the study leader of the project. AL took part in algae identification and in article preparation.

Disclaimer

The views expressed in the submitted article are the authors' own and not that of their institution.

Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

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Plant diversity and conservation value of wetlands along a rural–urban gradient

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Background: Wetlands are the most threatened ecosystem in South Africa despite the range of ecosystem goods and services they provide. A significant cause of wetland destruction and degradation is a lack of understanding, by planners, policymakers and developers, of their ecological and socio-economic importance.

Objectives: This study assessed the floristic composition and diversity of wetlands in the former Tlokwe Municipal area along a rural–urban gradient.

Methods: Fourteen wetland sites were surveyed along an urbanisation gradient. Vegetation surveys were done in quadrats along transects in each wetland recording the cover-abundance of each species. The data were analysed by using ordinations, similarity percentages, and the adjusted Floristic Quality Assessment Index.

Results: Overall, the proportional species composition of urban and rural wetlands was mainly similar. Trends indicated that the alpha diversity increased with both habitat size and heterogeneity along a rural–urban gradient. In all wetlands, indigenous species were the most abundant, with the highest score in the largest urban wetland. The floristic quality varied widely along the gradient with none of the sites in pristine condition.

Conclusion: The similarity in species composition and floristic quality of the wetlands, as well as the high levels of indigenous species richness, indicated that urban wetlands are worthy of conservation. However, the signs of disturbances and the presence of alien species means that restoration strategies need to be implemented to improve the quality of the wetlands.

Keywords: wetlands, rural–urban gradient, plant diversity, conservation value, floristic quality.

Introduction

Wetlands play an essential role in biodiversity conservation and in the supply of ecosystem services to humanity (Ramsar Convention Secretariat 2013). They fulfil several ecosystem services such as climate regulation, carbon storage, water reservoirs, runoff containment and flood risk reduction (e.g. Cimon-Morin & Poulin 2018; McInnes & Everard 2017). Moreover, they filter pollutants, conserve unique biodiversity, and act as a refuge for species (e.g. Bateganya et al. 2015; McInnes & Everard 2017). Important cultural ecosystem services include increased well-being of residents, eco-tourism, recreation and environmental education (e.g. Pedersen et al. 2019; Ramírez & Santana 2019).

History showed us that since the Iron Age, extensive drainage of the land took place so that it could be utilised for other purposes such as agriculture and settlements (Everard 1997; Hoeksema 2007). Land drainage happened due to an established idea that wetlands were only sources of disease and danger with no intrinsic value in themselves (Purseglove 1989). The Ramsar Convention of 1971 was the primary catalyst for the recognition of the importance of wetlands, and lobbied for global action towards their protection. However, Hettiarachchi et al. (2015) argue that this framework has key weaknesses that contribute to failures in urban wetland governance. Wetlands in urban areas are often regarded as wastelands (Panuccio et al. 2017), and subsequently, urbanisation is recognised as a significant cause of wetland loss (Panuccio et al. 2017). Not only can urban development cause destruction of wetlands, but it often also alters hydrological cycles, increases pollution that transforms wetlands, and influences species composition and species diversity (e.g. Baldwin 2011; Ehrenfeld 2000).

Local perceptions and the direct use of wetlands in urban areas vary. In an urban study in Canada, where residents did not visit local wetlands regularly, they still identified with the aesthetic value of wetlands and its importance as a habitat for biodiversity (Manuel 2003). In Cape Town, residents placed a high value on the provisioning services, mainly grazing for livestock, supplied by a peri-urban wetland and they derived 82% of their income from this wetland (Lannas & Turpie 2009). Wetlands were also found to be critical in reducing urban wastewater pollution in areas with malfunctioning or inadequate treatment plants (Bateganya et al. 2015). Moreover, wetland planning is seen as a critical element to be included in urban master plans due to its beneficial functions of flood control, water purification, microclimate regulation, and aesthetic and cultural value (Jia et al. 2011).

Notwithstanding the benefits mentioned above, urban wetlands are also important in urban biodiversity conservation. A study undertaken in Rome, Italy, on the importance of urban wetlands as a habitat for birds, recorded regular observations of species of conservation concern (Panuccio et al. 2017). Construction of urban wetlands in Greensboro, North Carolina, increased bat species richness and diversity (Parker et al. 2018). In addition, in Canada, some urban stormwater ponds had the same plant species, dragonfly and damselfly assemblages as natural ponds, which underlines the importance of urban wetlands to enhance local biodiversity (Perron & Pick 2020). Moreover, Semlitsch and Bodie (1998) have established that even if small or isolated, wetlands are integral for connectivity and maintaining biodiversity.

In South Africa, Working for Wetlands (2019) estimates that between 35% and 60% of the country's wetlands have been destroyed through drainage for crops and pastures, poorly managed burning regimes, overgrazing, disturbances to wetland soils, vegetation clearing as well as industrial and urban development (including mining activities). The latest National Biodiversity Assessment described wetlands as the country's most threatened ecosystem, stating that 88% of wetland areas are threatened and less than 2% are well protected (Skowno et al. 2019). Realising the importance of wetlands in South Africa, recent research efforts include the National Wetland Vegetation Database (Sieben et al. 2014) and the updated National Wetland Map 5 (van Deventer et al. 2020). Urban wetlands in South Africa have also seen an increase in research efforts and realisation of their importance, e.g. phytosociological studies of urban wetlands in Potchefstroom (Cilliers et al. 1998) and the Durban municipal area (Roberts 1993), the monetary valuation of provisioning services in a peri-urban wetland in Cape Town (Lannas & Turpie 2009), amphibians in urban wetlands (Kruger et al. 2015), health effects in fish in wetlands in Soweto (Bengu et al. 2017), wetlands as a habitat for birds (Calder et al. 2015), and the detrimental effects of urban development on wetlands (Govender-Ragubeer et al. 2014). The current study aimed to add to the developing body of knowledge on urban wetlands in South Africa. The primary objective was to assess the floristic composition, quality and diversity of wetlands in the former Tlokwe Municipal area along a rural–urban gradient. The specific research questions were: (1) do urban and rural wetlands differ based on their floristic composition and quality? and (2) are the local urban wetlands worthy of conservation?

Materials and Methods

Study area

The study was carried out in the former Tlokwe Municipal area, which now forms a part of the larger, recently amalgamated, JB Marks Local Municipality. The former Tlokwe Municipal area covers 2 672 km^2, which includes the urban area of Potchefstroom and its rural surroundings (Figure 1) and is located in the North West Province of South Africa. The population estimate of the study area was 179 604 in 2018 (JB Marks Local Municipality 2018). Research on the land-use transformation in the study area indicated significant changes in the cover of natural and urban areas over a period of 61 years (Pretorius et al. 2013). This inventory revealed a 23% increase in urban land coverage and a 68% increase in cultivated land-uses, decreasing the coverage of natural habitats by 12% and impacting the coverage of wetlands in the area.

The mean annual rainfall of the study area is 600 mm, falling mainly in the summer months with average temperatures between 0°C and 30°C, and frequent frost in winter (www.weathersa.co.za). The Mooi River flows through Potchefstroom and includes rural upstream and downstream segments with a city segment influenced by decades of urban development. There are various dams situated in the Mooi River system of which the Potchefstroom Dam and Boskop Dam are located

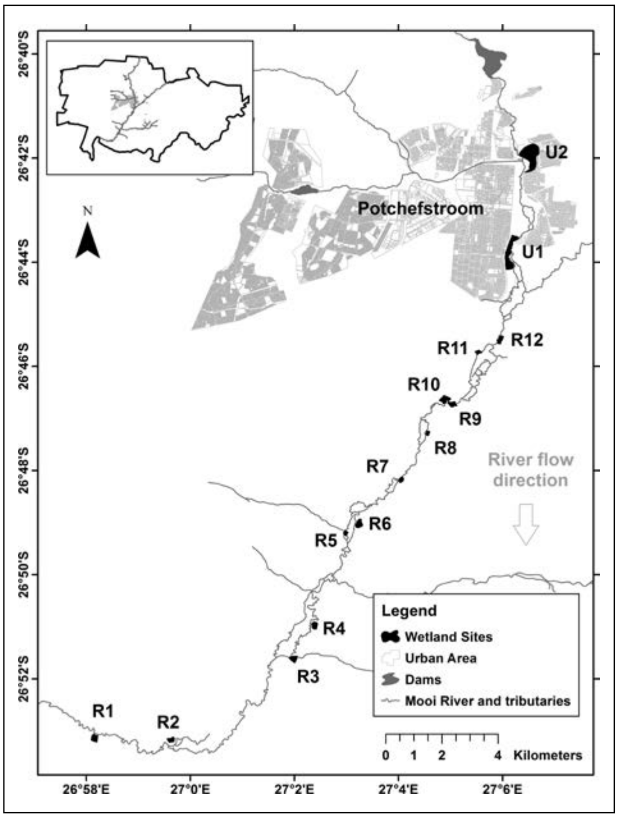

Figure 1. Study area indicating the urban area of Potchefstroom, its rural surroundings and the 14 wetland study sites. Inset map shows the size and location of the urban area and Mooi River within the former Tlokwe Municipal area.

within the municipal area. The water of the Mooi River system is contaminated by agricultural and mining pollutants, of which the impact of mining is of particular concern to the water quality in the system (Barnard et al. 2013). A recent study on phytoplankton assemblages and the measurement of physico-chemical variables in the Mooi River and its tributaries, confirmed that the system was polluted and that the water quality is declining (Koekemoer et al. 2021).

The study area lies within the Grassland Biome on the high central plateau of South Africa and at the confluence of three vegetation types: the Carletonville Dolomite Grassland, the Rand Highveld Grassland, and the Andesite Mountain Bushveld (Mucina et al. 2006). The wetlands in the study area are classified as grass lawn wetland vegetation (Sieben et al. 2016) and temperate grassy wetland vegetation (Sieben et al. 2017).

Site selection

All possible wetland sites along the Mooi River (excluding its tributaries) within the study area (Figure 1) were identified using satellite imagery. All sites accessible via roads and on private property, where owners granted permission, were visited. Wetlands chosen for this study were those ecosystems defined by the National Water Act (No. 36 of 1998) (South Africa 1998), as 'land that is transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, or land which is periodically covered with shallow water, and land which, under normal circumstances, supports or would support vegetation typically adapted to live in saturated soils'. To delineate physical wetland boundaries of this study, wetland vegetation was used as an indicator. Fourteen wetland study sites were selected from the city and downstream segments of the Mooi River (Figure 1, Table 1). Approximately 80% of all the downstream wetlands were included in this study. Table 1 shows the selected wetland sites with their respective sizes and the number of transects surveyed per wetland.

Quantification of the rural–urban gradient

The rural–urban gradient was objectively quantified using four urbanisation measures namely: edge density, percentage vegetation cover, percentage urban land cover, and density of dwellings as selected by van der Walt et al. (2014) using Hawth's analysis tools version 3.27 (Beyer 2007) and ArcGIS 10 (ESRI 2010). The urbanisation measures were calculated for matrix areas represented by a 500 m buffer surrounding each selected wetland. Edge density is the sum of the length (m) of all edge segments divided by the area (in hectares) (McGarigal & Marks 1995). Percentage vegetation and urban land cover were both calculated as the total area covered by each land cover type divided by the total matrix area multiplied by 100 (McGarigal & Marks 1995). Urban land cover was digitised as all impervious built-up surfaces within the matrix, e.g. roads, buildings. The density of dwellings was calculated by digitised point counts of all the buildings in the matrix divided by the matrix area (McGarigal & Marks 1995).

Hierarchical, agglomerative cluster analysis in PRIMER 6 software (Clarke & Gorley 2006) and a subsequent Non-metric Multi-Dimensional scaling (NMDS) ordination indicated two clear groupings in the data (Figure S1 and S2, Supplementary material). Table 1 provides the specific urbanisation measure values for each selected wetland study site. A Pearson r correlation matrix was calculated to see whether one measure could be used as a proxy to represent the rural–urban gradient. All the measures correlated highly with each other, so we chose the percentage urban land cover to represent the gradient as the most intuitive measure (Table S1, Supplementary material). Based on the NMDS and cluster analysis, two sites were classified as urban and 12 as rural. The rural wetlands are all situated in matrix areas that have less than 3% urban land cover (Table 1), and the two urban sites had a percentage urban land cover ranging between 35 and 45%.

Table 1. The characteristics of each wetland site and the values of the urbanisation measures used to categorise the sites into urban and rural sites. R, rural sites; R1, furthest away from the city; R12, closest to the city; U, urban sites

					Urbanisation measures			
Site	Size (ha)	NR of Transects	Landuse	Management type	Percentage urban land cover	Edge density	Percentage vegetation cover	Density of dwellings
R1	3.79	9	Rural agriculture	Grazing	2.43	263.765	87.93	0.256
R2	2.58	5	Rural agriculture	Grazing	1.25	293.14	87.59	0.107
R3	3.41	5	Rural agriculture	Grazing	2.75	188.98	90.57	0.121
R4	3.21	4	Rural agriculture	Grazing	0.04	218.076	99.62	0.018
R5	1.44	3	Rural agriculture	Grazing	0.03	130.043	96.72	0
R6	4.24	4	Rural agriculture	Grazing	0.51	177.39	94.92	0
R7	1.76	4	Rural agriculture	Grazing	2.46	217.995	96.29	0.201
R8	1.14	3	Rural agriculture	Grazing	1.51	230.765	93.83	0.05
R9	2.95	6	Rural agriculture	Grazing	1.63	218.115	96.22	0.051
R10	4.79	10	Rural agriculture	Grazing	0.72	201.93	97.5	0
R11	1.47	3	Rural agriculture	Grazing	1.97	205.553	95.5	0.086
R12	2.85	6	Rural agriculture	Grazing	1.98	266.72	93.53	0.094
U1	17.01	30	Urban	Grazing and Bird Sanctuary	35.9	397.045	63.79	3.66
U2	31.58	38	Urban	Grazing and Recreational activities	43.77	477.458	55.34	3.661

Vegetation surveys

Vegetation surveys were conducted from January to March 2014, during the flowering season of most plants. Plant species composition and abundance within the wetlands were determined by laying 100 m line transects across each wetland (Ruto et al. 2012). Transects were aligned along the longest axis of each wetland. Where sites were wide enough, adjacent transects were sampled parallel to one another, 20 m apart. The number of transects per selected wetland was determined by the size of the wetland under observation. A minimum of three transects were done per wetland (since the smallest wetlands could only fit three transects with 20 m between each transect). The largest wetland (U2) had 38 transects (Table 1). The presence and estimated percentage crown cover of each plant species were determined in a 1 m^2 quadrant placed at 10 m intervals along the 100 m transects (Ruto et al. 2012) situated in homogenous areas of each wetland site. A total of 130 transects (1 254 quadrants, not all transects had 10 sample plots due to open water areas) were sampled in the 14 wetland sites.

The soft traits used in this study included the origin of each species (indigenous/alien), life history (annual/perennial), growth form (tree, shrub, forb, graminoid and geophyte) and wetland indicator status. The wetland indicator status divides plants into categories based on their expected frequency of occurrence in wetlands namely obligate wetland (>99%), facultative wetland (67–99%), facultative (34–66%), facultative upland (1–33%) and upland (<1%) (Tiner 2006).

Data analysis

The floristic composition of each of the wetlands was compared using NMDS. The ordination was performed using the Primer 6 software (Clarke & Gorley 2006). The average percentage cover of species per transect was used as input for the ordination. The sample data was first square root transformed to allow a greater contribution from the rare species, and then sites were compared using the Bray-Curtis dissimilarity coefficient. To determine the percentage dissimilarity between urban and rural sites based on the cover-abundance data, a similarity percentages (SIMPER) analysis was done in Primer 6. This analysis compared sites based on respective species composition and also indicates which species account for dissimilarities between sites.

The Wetland Index Value or WIV for each wetland site surveyed (i.e., community weighted mean) were calculated using the abundance of plant species and their ecological index value based on their wetland indicator status (Carter et al. 1988). The WIV provides a useful way of interpreting the status of wetlands based on their vegetation composition and is based primarily on the relevant species' wetland indicator status (Cowden et al. 2014). The values represent a wetness gradient with values less than 2.5 indicating a true wetland and values above 3.6 a non-wetland area (Carter et al. 1988)

Data on the abundance of plant species and their classification status were used to determine the adjusted Floristic Quality Assessment Index (adjFQAI), as defined by Miller and Wardrop (2006). The adjFQAI addresses the problem of sensitivity to species richness and the contribution of non-native species (Miller & Wardrop 2006). The adjFQAI is an evaluation procedure that indicates the quality of the wetland habitat based on the relative abundance of indigenous, weedy, pioneer or alien invasive species within each surveyed site. Moreover, the adjFQAI calculates the percentage of the maximum value attainable by the site if all the species present were low tolerance indigenous species indicative of pristine wetland communities (Miller & Wardrop 2006). Species were assigned a 'coefficient of conservatism' that is 'a subjective rating indicating a species' preference for non-degraded natural communities' (Tiner 1999). Within the selected wetland sampling sites, each plant species was allocated a specific coefficient of 0 to 10 based on its conservation value relative to other native species in the surrounding area. Values ranged between alien species (0) and indigenous species with very low tolerances, to disturbance and high fidelity to habitat integrity (10) (Miller & Wardrop 2006). The allocation of the coefficient was based on available literature (Retief & Herman 1997; Van Ginkel et al. 2011).

Results

Plant species composition and diversity

The total number of species recorded in the wetlands along the rural–urban gradient was 102 (for the complete species lists and the list of invasive alien species recorded in the sites refer to Tables S2 and S3 in the supplementary material). Rural sites had a slightly higher gamma diversity than urban sites, but proportionately their overall species composition, diversity, origin, life history and wetland indicator status types were mostly similar (Table 2).

The analysis of the similarity between urban and rural sites in the current study indicated that the two urban sites were 67% similar, with the 12 rural sites displaying only 45% similarity. The average dissimilarity between urban and rural sites was 62%. Table 3 indicates that 22% of the dissimilarity between urban and rural sites in this study was due to the difference in abundance

Table 2. Plant species diversity, traits and wetland indicators of urban and rural land-use sites. The species richness (SR) and percentage contribution (%) of each category are listed

		Urban		Rural	
Category	**Trait**	**SR**	**%**	**SR**	**%**
Gamma diversity	Total per land use type	69	-	78	**-**
Origin	Indigenous	47	68.1	56	71.8
	Alien	22	31.9	22	28.2
Growth Form	Geophyte	1	1.4	2	2.6
	Graminoid	15	21.7	21	26.9
	Forb	49	71	53	67.9
	Shrub	1	1.4	1	1.3
	Tree	3	4.3	1	1.3
Life history	Annual	18	26.1	23	29.5
	Perennial	51	73.9	55	70.5
Wetland indicator species	Obligate wetland	29	42	27	34.6
	Facultative wetland	16	23.2	19	24.4
	Facultative	12	17.4	18	23.1
	Facultative upland	9	13	14	17.9
	Upland	3	4.3	0	0

of four species. Of the four species, *Carex glomerabilis* Krecz., *Paspalum dilatatum* Poir. and *Typha capensis* (Rohrb.) N.E.Br. almost exclusively occurred only in the two urban sites, whereas *Cyperus longus* L. had higher abundances in the urban sites than in the rural sites. The first three species were also listed as historically occurring in the wetlands of the region (Louw 1951).

Table 3. SIMPER analysis indicating the species which contributed to 50% of the dissimilarity between urban and rural sites. Listed are the average abundance, percentage contribution, and the cumulative percentage contribution of each species. The asterisk indicates an alien species

Species	**Urban average abundance**	**Rural average abundance**	**Percentage contribution**	**Cumulative percentage contribution**
Carex glomerabilis	2.97	0.17	6.66	6.66
*Paspalum dilatatum**	3.11	0.65	5.85	12.51
Cyperus longus	3.95	1.81	5.17	17.68
Typha capensis	2.01	0.12	4.46	22.14
Cyperus laevigatus	2.11	1.08	4.18	26.32
Cyperus fastigiatus	1.29	2.05	4.08	30.4
Paspalum distichum	2.05	2.03	3.83	34.23
Leersia hexandra	3.16	1.88	3.5	37.73
Echinochloa holubii	0.11	1.6	3.47	41.2
Cynodon dactylon	1.78	0.35	3.41	44.62
Falkia oblonga	2.88	1.82	3.34	47.95
Berula erecta	1.51	0.13	3.24	51.19

Overall, the ordination of average cover-abundance per transect per site indicated no distinct differences between urban and rural sites (Figure 2). However, groupings within the sample sites are visible, indicating differences in species composition. The closer similarity of some U1 transects with the rural transects, indicated the transitional nature of this site along the gradient. The reason for this pattern might be the location of this site on the periphery of the urban area.

Due to the small number of wetland sites and the absence of sites representing the full range of the gradient (rural sites were limited to 0–3% urban land cover, while urban sites had 35–45% urban land cover), we did not do any statistical analyses on correlations between sites along the gradient. However, the influence of urbanisation on wetlands was explored by arranging the sites along the rural–urban gradient from the site with the lowest percentage urban land cover to one with the highest percentage urban land cover in all the following graphs.

The alpha diversity graph indicates that there was an overall trend of increased species richness along the urbanisation gradient (Figure 3a). The difference in sizes of the various sites partially explains this phenomenon, especially with regards to the urban wetlands (Figure 3c). The same trend is not apparent in the average species richness per transect per site (Figure 3b). Beta diversity was calculated as (i) the average beta diversity per site between the 12 rural sites; (ii) the average beta diversity between the two urban sites and all the rural sites; and (iii) the beta diversity between the two urban sites (Figure 4a). The graph indicates a visible, increasing trend of more unique species recorded as urbanisation

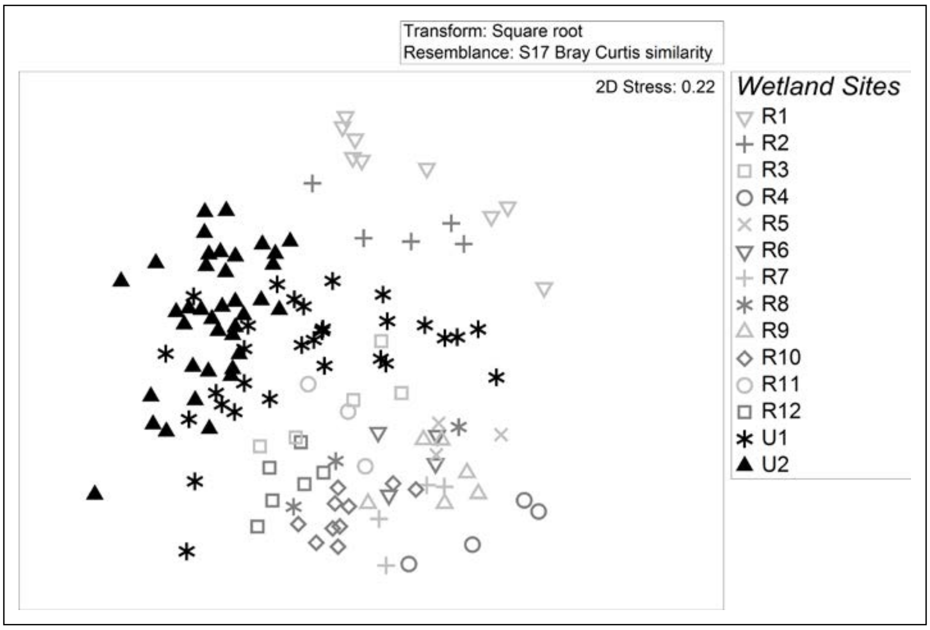

Figure 2. NMDS ordination for the average cover-abundance per transect per site of all species.

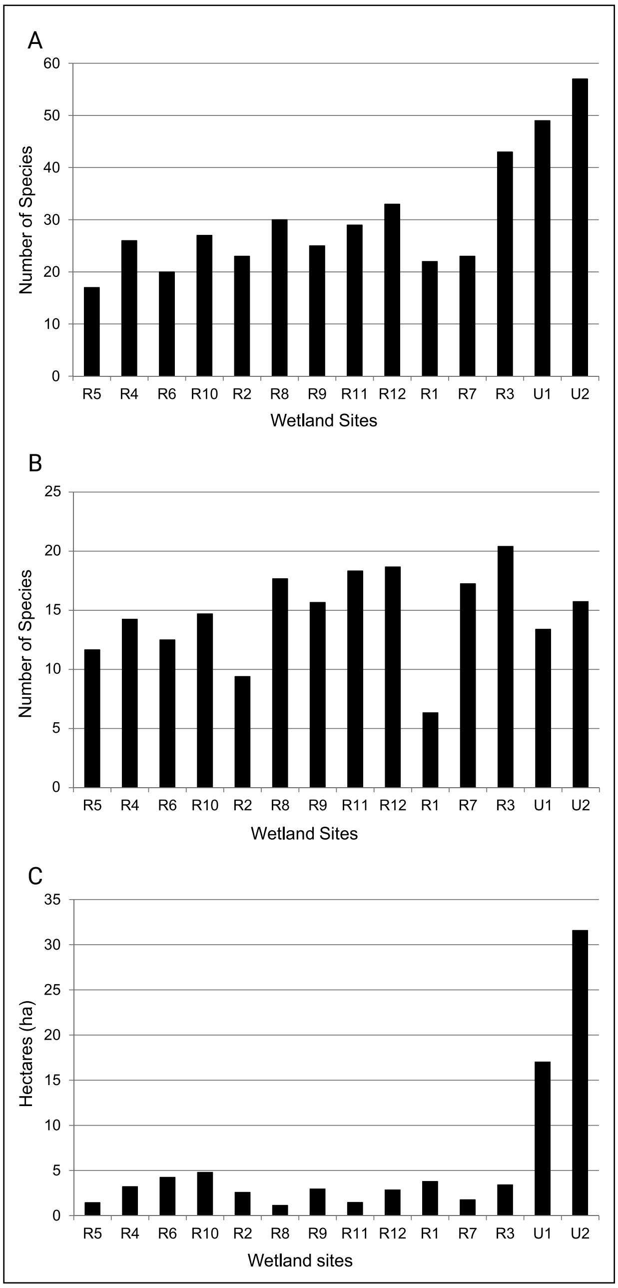

Figure 3. A, Total number of species per wetland site (alpha diversity); B, the average species richness per transect for each site; C, the size of each wetland; arranged along a gradient of increasing percentage urban landcover.

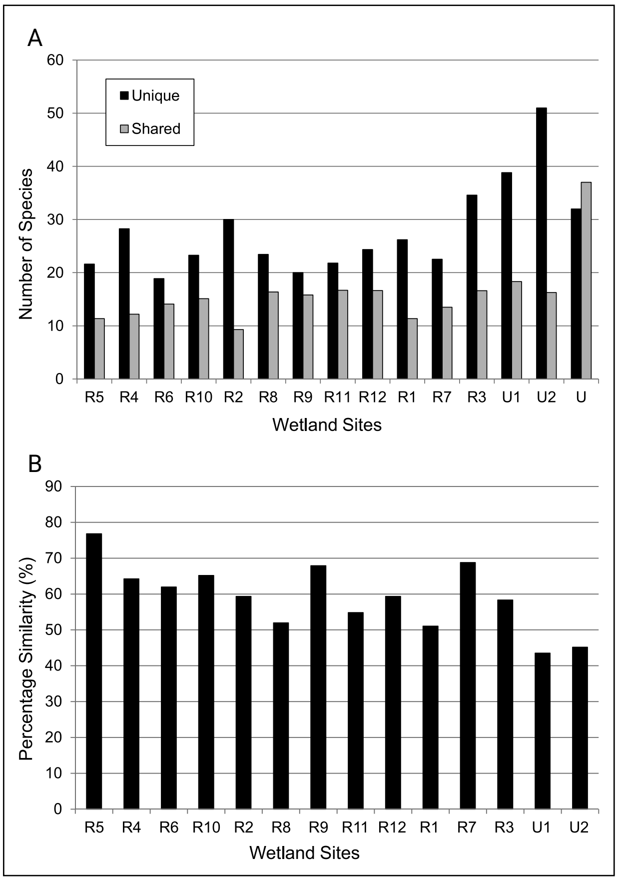

Figure 4. A, Beta diversity between sites (calculated as the average between all the rural sites (R1–R12), the average between the two urban sites and all the rural sites (U1 and U2), and between the two urban sites (U)); B, the SIMPER analysis results of the average similarity of the transects in each wetland site; arranged along a gradient of increasing percentage urban landcover.

increases, linked to both an increase in size and habitat heterogeneity (Kallimanis et al. 2008). The graph also indicates that the two urban wetlands shared more species than having unique species, which was reversed in the rural wetlands. This observation reflects the results of the SIMPER analysis reported earlier, which indicated that urban sites were more similar than rural sites. However, analysis of the similarity of the transects of each respective site indicated a trend of decreased similarity of the sites as the percentage urban land cover increased (Figure 4b). The ordination also shows that the rural sites were not closely associated with each other (Figure 2). The high alpha diversity of urban sites is supported by the low percentage of similarity of its transects within the sites, indicating heterogeneity (Figure 4b).

Functional diversity

The wetland index values indicated that all the sites are true wetlands with values well below 2.5 (Cowden et al. 2014) and were, therefore, comparable (Figure 5a). The overall cover-abundance of vegetation in each site varied with no apparent link to a trend along the gradient (Figure 5b). The percentage composition of the specific growth forms, and the wetland indicator types, showed no marked differences along the gradient (Figure 5c

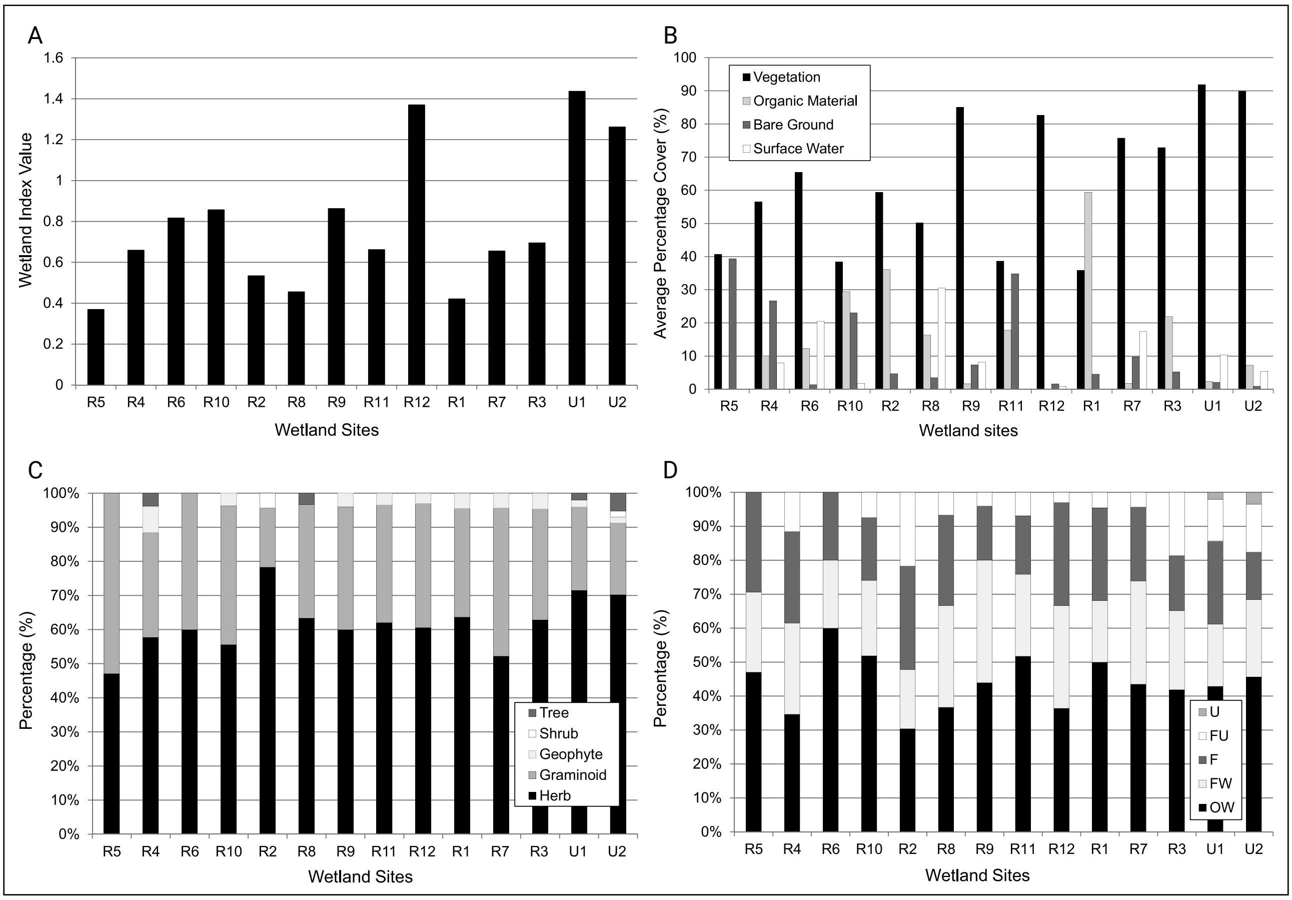

Figure 5. A, Wetland index values (WIV) of each site; B, the average site cover descriptions; C, the percentage average growth form distribution at each site; D, the average functional diversity per site (upland (U), facultative upland (FU), facultative (F), facultative wetland (FW), obligate wetland (OB)); arranged along a gradient of increasing urban landcover.

and d). The higher wetland indicator values of the urban wetlands indicated the presence of more facultative upland and upland species in comparison to the other wetlands (Figure 5d). The trends of the vegetation cover-abundance graph and the wetland indicator graphs are very similar, indicating that the higher cover-abundance of vegetation might signify drier conditions.

Quality

The origin of wetland species indicates the quality of the habitats. In all sites, the indigenous species dominated proportionately based on the total average cover of species per site (Figure 6a and c). A visible trend of higher indigenous and alien species richness with increased urban land cover was also observed. The urban sites, specifically, had a much higher alien species richness (Figure 6b). The cover-abundance of alien species showed no visible trend along the gradient. The greater the difference between the number of indigenous and alien species, the higher was the adjusted floristic quality assessment index (adjFQAI) (Figure 6d). Sites with the highest proportion of indigenous species (Figure 6a) had the highest adjFQAI values. There was no visible trend of any influence of position along the gradient on the quality of the sites.

Discussion

The effect of the urbanisation gradient was only visible in the trends of overall species richness and both indigenous and alien species richness. We acknowledge that the larger size of the urban wetlands affected increased species richness (Kallimanis et al. 2008). However, the high species richness of the most urbanised rural site had no relation to its size. Moreover, this site (R3) had a higher indigenous species richness than the smaller of the two urban wetlands (U1). Kallimanis et al. (2008) showed that higher species richness is also linked to increased habitat diversity. The only other phenomenon that showed a possible linkage to the amount of urban land cover was the analysis of the similarity of the transects within each site, indicating a downward trend with an increased heterogeneity along the gradient. There was no link between the wetland indicator values and the percentage of urban land cover in this study, indicating that site-specific factors were involved. This observation was also true for the quality of the wetlands indicated by the adjusted floristic quality assessment index.

Bare ground and high organic material cover seemed to explain the low species richness of some rural sites. A dense litter layer is a general constraint to the species

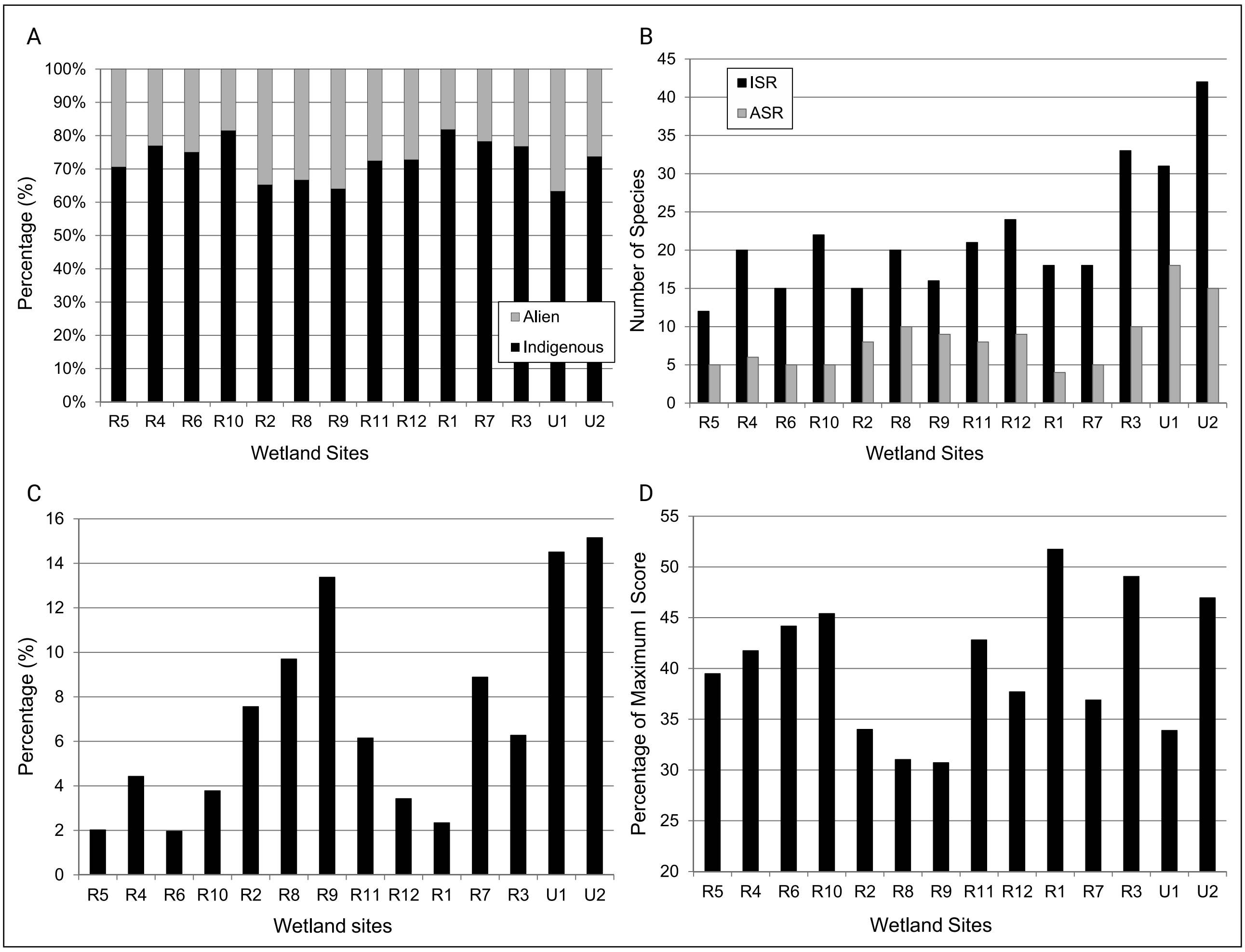

Figure 6. A, Percentage distribution of alien and indigenous species per site; B, the indigenous (ISR) and alien (ASR) species richness per site; C, the percentage of the total average cover of all alien species per site; D, the associated adjusted Floristic Quality Assessment Index values (adjFQAI) of each site; arranged along a gradient of increasing percentage urban landcover.

richness of wetlands (Doherty & Zedler 2014), where the high cover percentage of organic material in some rural wetlands could be one of the reasons why they have a lower number of species. According to Cilliers et al. (1998), a large number of plant communities occurred in these urban wetlands suggesting high heterogeneity. Moreover, both urban wetlands serve as urban stormwater discharges with channels dug into the sites. These channels increase the influx of pollution and alien plant propagules into the wetlands. The overabundance of seed sources in urban areas could also increase species richness in these sites. However, the overall high similarity analysis of the two urban sites (67%) in comparison to rural sites might support the findings of Ding et al. (2019) in research done on 35 cities in China. They found that comparisons of floristic similarity of aquatic macrophytes were much higher in the urban communities than in the rural communities, suggesting biotic homogenisation. Furthermore, they state the high proportion of shared common species as a possible reason (Ding et al. 2019).

Although the aim of this study was neither to classify wetland vegetation nor to compare the species composition and abundance of the studied wetlands with previous studies of urban (Cilliers et al. 1998) and rural wetlands (Louw 1951), the results do suggest some changes to these wetlands over the years. Firstly, the *Cynodon dactylon* (L.) Pers. invasive community had probably increased in area as both urban wetlands still have continuous grazing and trampling pressures by cattle and horses. Weedy species, such as *C. dactylon*, are well adapted to these disturbed conditions as they can replace damaged tissues quickly, and due to their rhizomatous nature, they are good colonisers (Cilliers et al. 1998; Sieben et al. 2014). Secondly, the high abundance of *Phragmites australis* (Cav.) Steud. and *T. capensis* in certain areas of the urban wetlands could indicate an increase of cover in the two communities dominated by these species. This dominance was probably due to the urban stormwater runoff outlets into the wetlands, favouring these species which are well adapted to waterlogged conditions. These species are also well adapted to eutrophication (Sieben et al. 2014). Although urbanisation has influenced wetlands in Potchefstroom, it is difficult to determine the extent thereof as no detailed studies were done of reference conditions. Louw (1951) has already indicated the effect of disturbances, such as the artificial drainage of the wetland areas due to irrigation. A large number of indigenous wetland species, such as the free-floating hydrophytes and many of the marshland species described by Louw (1951), were not encountered in the rural and urban wetlands of the current study. The reed swamp communities dominated by *P. australis* and *T. capensis* were also quite extensive in the rural wetlands described by Louw (1951), but an invasion by *C. dactylon* was not mentioned at all.

Wondie (2018) found in a study in Ethiopia, that although the impaired urban and agricultural wetlands had a higher plant species diversity than the natural wetlands, the majority of these plant species were alien weeds and upland species, outcompeting the native species, which are ecologically and socio-economically important. They described the main reasons to be direct and indirect anthropogenic activities, including waste discharges through streams and ditches in towns. Wastewater management is a huge challenge in cities in sub-Saharan Africa, and Bateganya et al. (2015) explained that urban wetlands are considered as natural features to aid conventional municipal wastewater treatment plants that are ineffective due to overloading and poor maintenance. Other studies have also indicated that urban wetlands usually have a higher alien species richness than rural wetlands (Albert & Minc 2004; Dallimer et al. 2012; Dolan et al. 2011). The higher alien species richness was also true for the two urban wetlands in this study. However, the most urbanised wetland had the highest indigenous species richness of any of the sites. The high species richness was certainly linked to the size of the wetland. The results of the adjusted floristic quality assessment index indicated that none of the wetlands is in a pristine condition (Miller & Wardrop 2006). However, in all of the sites, indigenous species constitute more than 60% of the species richness and more than 85% of the cover-abundance. Therefore, if correct remediation and ecological restoration techniques were to be applied, these wetlands can be restored (Baldwin 2011) to provide a variety of ecosystem services (Cilliers et al. 2013). Urban wetlands are often perceived as of poor quality and highly disturbed (Panuccio et al. 2017), but in the current study, the largest urban wetland also had the highest indigenous species richness with the third-highest floristic quality value. The high indigenous species richness means that in this study, urban wetlands are vital for the conservation of local biodiversity and highlights the value that urban wetlands have in enhancing and supporting biodiversity (Baldwin 2011). Wetland plants are adapted to long-distance wind and water dispersal (Soomers et al. 2013). Therefore, adequately connected sites can harbour high species richness despite fragmentation pressures (Soomers et al. 2013). However, Cimon-Morin and Poulin (2018) remind us that it is a challenge to conserve small urban wetlands as decision-makers often do not recognise their importance both in terms of ecosystem services and biodiversity within the larger wetland system.

The limitations of this study included a lack of access to all potential sites and sampling only within the former Tlokwe Municipal area. Increasing sampling to upstream and other nearby urban wetlands, and incorporating the landscape history of the sites, would clarify identified trends and provide a better understanding of the local drivers of wetland diversity in the area.

Conclusions

This small, localised study identified possible trends due to the impact of urbanisation on wetland communities along a rural–urban gradient. However, the urbanisation gradient did not correlate with wetland indicator values or the floristic quality of the sites indicating that other drivers were responsible for the observed patterns. Nevertheless, our study highlighted the potential importance of urban wetlands for the conservation of biodiversity. In our study, the much larger urban wetlands had the highest and third-highest indigenous species richness as well as a higher floristic quality than most of the rural sites. However, the signs of disturbances and the presence of alien species means that restoration strategies need to be implemented to improve the quality of the wetlands. Notwithstanding their essential role in stormwater discharge already implemented in the municipality, urban wetlands have multiple other ecosystem service benefits that in combination with their high biodiversity, make them essential to conserve.

Authors' contributions

MJDT assisted with fieldwork, conducted data analyses and wrote half of the manuscript; CDP did the study as a masters' project, she did the field work and wrote parts of the current manuscript; SSC planned and coordinated the study, assisted with fieldwork and wrote half of the manuscript.

Disclaimer

The views expressed in the submitted article are our own and not an official position of the institution or funder.

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Supplementary material

Correlation matrix and species lists

Table S1. Correlation matrix of the urbanisation measures to determine their association with each other

	Percent urbanisation	Edge density	Percent vegetation	Density of dwellings
Percent urbanisation	1			
Edge density	0.903076	1		
Percent vegetation	-0.97182	-0.93049	1	
Density of dwellings	0.993281	0.891734	-0.96461	1

Table S2. List of all the species recorded in this study. Indicated are the respective number of transects in which the species were found and their representative percentage occurrence in urban and rural sites

Species name	No. of urban transects	urban % occurrence	No. of rural transects	rural % occurrence
Agrostis continuata	2	2.9	0	0.0
Albuca setosa	0	0.0	2	3.2
Alternanthera sessilis	0	0.0	27	43.5
Ambrosia psilostachya	11	16.2	0	0.0
Ammi majus	3	4.4	0	0.0
Andropogon appendiculatus	0	0.0	4	6.5
Anthospermum herbaceum	0	0.0	5	8.1
Asparagus laricinus	0	0.0	1	1.6
Aster squamatus	2	2.9	22	35.5
Berkheya setifera	1	1.5	2	3.2
Berula erecta	27	39.7	6	9.7
Bidens pilosa	0	0.0	1	1.6
Bidens bipinatta	0	0.0	1	1.6
Brachiaria eruciformis	3	4.4	49	79.0
Carex acutiformis	3	4.4	0	0.0
Carex glomerabilis	58	85.3	6	9.7
Cichorium intybus	3	4.4	0	0.0
Cirsium vulgare	4	5.9	6	9.7
Chenopodium album	0	0.0	1	1.6
Conyza bonariensis	0	0.0	6	9.7
Cotula australis	0	0.0	1	1.6
Crinum bulbispermum	7	10.3	13	21.0
Cynodon dactylon	36	52.9	12	19.4

Table S2. List of all the species recorded in this study. Indicated are the respective number of transects in which the species were found and their representative percentage occurrence in urban and rural sites (continued)

Species name	**No. of urban transects**	**urban % occurrence**	**No. of rural transects**	**rural % occurrence**
Cynodon transvaalensis	1	1.5	14	22.6
Cyperus congestus	13	19.1	0	0.0
Cyperus eragrostis	0	0.0	3	4.8
Cyperus esculentus	0	0.0	2	3.2
Cyperus fastigiatus	18	26.5	36	58.1
Cyperus laevigatus	43	63.2	29	46.8
Cyperus longus	67	98.5	52	83.9
Cyperus marginatus	1	1.5	0	0.0
Echinochloa colona	0	0.0	8	12.9
Echinochloa holubii	7	10.3	42	67.7
Echinochloa pyramidalis	3	4.4	4	6.5
Eleocharis dregeana	17	25.0	9	14.5
Eragrostis curvula	0	0.0	4	6.5
Eragrostis heteromera	7	10.3	15	24.2
Eragrostis micrantha	0	0.0	2	3.2
Eragrostis plana	0	0.0	3	4.8
Euphorbia helioscopia	26	38.2	0	0.0
Falckia oblonga	32	47.1	44	71.0
Festuca caprina	4	5.9	3	4.8
Fuirena pachyrrhiza	0	0.0	2	3.2
Fuirena pubescens	0	0.0	1	1.6
Gleditsia triacanthos	6	8.8	0	0.0
Gomphrena celosiodes	1	1.5	0	0.0
Haplocarpha lyrata	0	0.0	1	1.6
Heliochrysum krausii	1	1.5	0	0.0
Hemarthria altissima	54	79.4	45	72.6
Hibuscus trionum	3	4.4	8	12.9
Hydrocotyla verticillata	1	1.5	0	0.0
Juncus punctorius	3	4.4	1	1.6
Juncus rigidus	2	2.9	1	1.6
Kniphofia ensifolia	6	8.8	3	4.8
Lactuca capensis	23	33.8	0	0.0
Lactuca inermis	16	23.5	0	0.0
Leersia hexandra	61	89.7	43	69.4
Lobelia thermalis	2	2.9	0	0.0

Table S2. List of all the species recorded in this study. Indicated are the respective number of transects in which the species were found and their representative percentage occurrence in urban and rural sites (continued)

Species name	No. of urban transects	urban % occurrence	No. of rural transects	rural % occurrence
Marsilea capensis	37	54.4	30	48.4
Medicago sativa	0	0.0	1	1.6
Melilotus alba	10	14.7	1	1.6
Mentha aquatica	5	7.4	0	0.0
Modiola caroliana	2	2.9	0	0.0
Moraea thomsonii	0	0.0	2	3.2
Oenothera rosea	12	17.6	9	14.5
Oxalis corniculata	0	0.0	1	1.6
Panicum coloratum	0	0.0	1	1.6
Paspalum dilatatum	62	91.2	16	25.8
Paspalum distichum	36	52.9	36	58.1
Pennisetum cladestinum	0	0.0	3	4.8
Persicaria decipiens	12	17.6	19	30.6
Persicaria lapathifolia	2	2.9	23	37.1
Persicaria senegalensis	0	0.0	2	3.2
Phragmites australis	26	38.2	4	6.5
Plantago lanceolata	8	11.8	9	14.5
Plantago major	5	7.4	5	8.1
Pycreus macranthus	18	26.5	12	19.4
Pycreus macrostachyos	9	13.2	5	8.1
Pycreus nitidus	2	2.9	0	0.0
Rumex crispus	43	63.2	43	69.4
Rumex lanceolatus	1	1.5	4	6.5
Salix babylonica	1	1.5	0	0.0
Schoenoplectus brachyceras	18	26.5	4	6.5
Schoenoplectus corymbosus	1	1.5	1	1.6
Sesbania bispinosa	3	4.4	3	4.8
Sesbania transvaalensis	0	0.0	11	17.7
Setaria incrassata	0	0.0	5	8.1
Setaria pallide-fusca	2	2.9	26	41.9
Sisymbrium thellungii	9	13.2	0	0.0
Solanum retroflexum	0	0.0	1	1.6
Sonchus oleraceus	1	1.5	4	6.5
Sonchus wilmsii	0	0.0	1	1.6
Sporobolus fimbriatus	4	5.9	0	0.0

Table S2. List of all the species recorded in this study. Indicated are the respective number of transects in which the species were found and their representative percentage occurrence in urban and rural sites (continued)

Species name	**No. of urban transects**	**urban % occurrence**	**No. of rural transects**	**rural % occurrence**
Taraxacum officinale	0	0.0	1	1.6
Typha capensis	29	42.6	4	6.5
Trifolium africanum	0	0.0	1	1.6
Trifolium repens	16	23.5	0	0.0
Verbena brasiliensis	4	5.9	0	0.0
Verbena bonariensis	1	1.5	2	3.2
Verbena officinalis	0	0.0	36	58.1
Veronica anagalis-aquatica	35	51.5	0	0.0
Xanthium strumarium	17	25.0	12	19.4

Table S3. List of the alien invasive species found in the wetland sites that are listed in the Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983) (CARA) and the National Environmental Management: Biodiversity Act (Act No. 10 of 2004) (NEM:BA) and their presence and cover abundance in the urban and rural transects respectively

Species name	**CARA**	**NEM:BA**	**% of urban transects**	**% of rural transects**	**urban average cover abundance per site**	**rural average cover abundance per site**
Cirsium vulgare	**1**	**1b**	5.882353	9.677419	0.027862	0.05027778
Gleditsia triacanthos	**2**	**1b**. Sterile cultivars or hybrids not listed	8.823529	0	0.0078947	0
Pennisetum clandestinum	Not listed	**1b** in Protected Areas and wetlands in which it does not already occur. Not listed elsewhere.	0	4.83871	0	0.01130268
Salix babylonica	**2**	Not listed	1.470588	0	0.0921053	0
Verbena bonariensis	Not listed	**1b**	5.882353	0	0.0058366	0.00277778
Verbena brasiliensis	Not listed	**1b**	0	58.06452	0.0107004	0
Xanthium strumarium	**1**	**1b**	25	19.35484	0.0841977	0.06470085

Urbanisation gradient

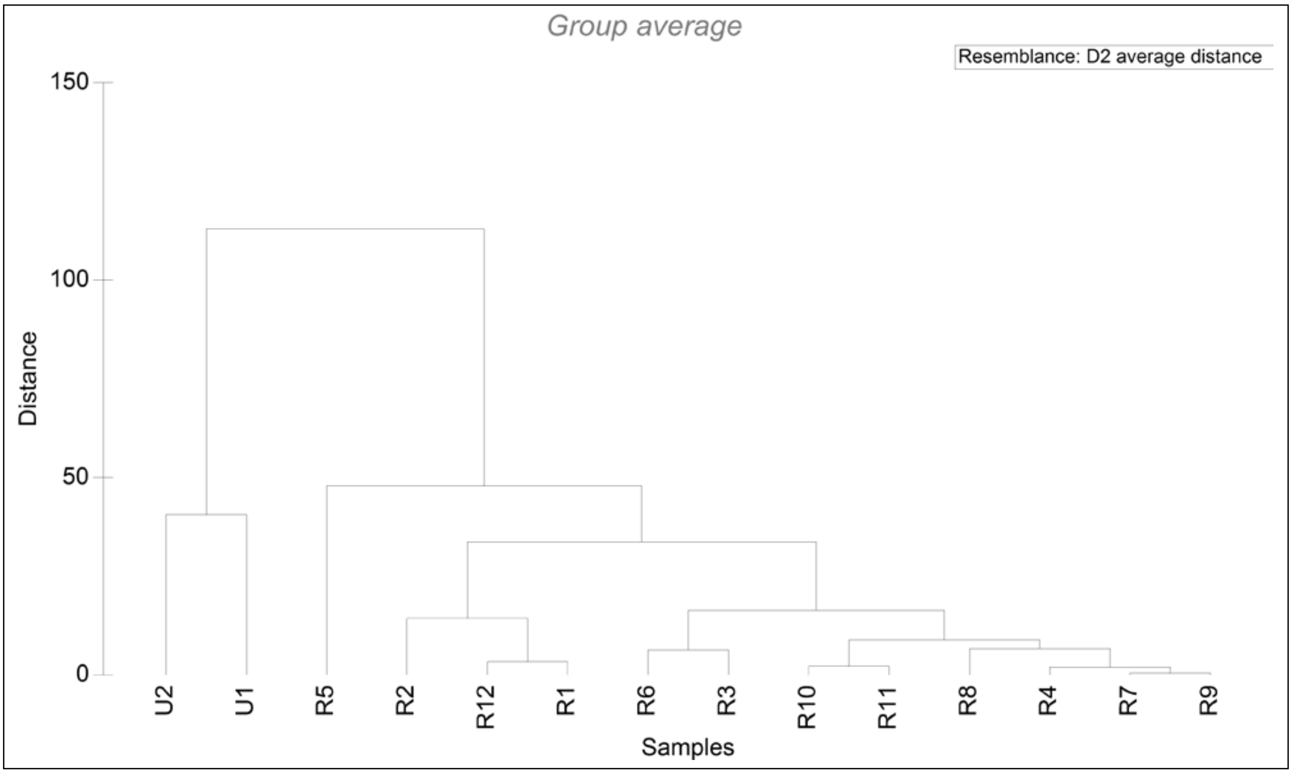

Figure S1. Cluster analysis results based on the urbanisation measures indicating clear grouping between the urban sites 1 and 2 and the rural sites.

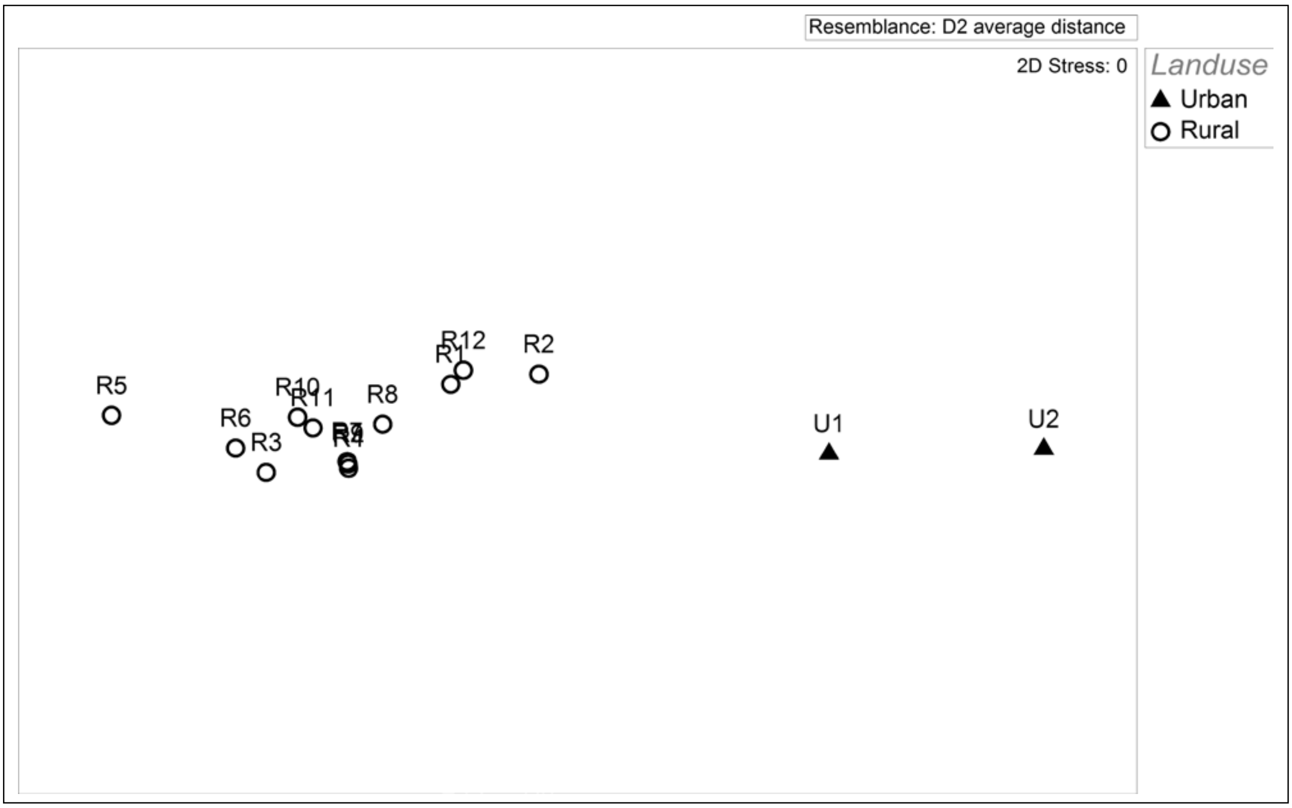

Figure S2. MDS ordination indicating the clear separation of the two land use groups based on the urbanisation measures.

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Diatom responses to river water quality in the Kruger National Park, South Africa

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Background: Although the Kruger National Park (KNP) is a protected area, it is not exempted from anthropogenically induced impacts, which often compromise river water flow and quality. Measures of river water quality in South Africa have conventionally been based on water chemistry as well as different ecological indicator groups such as fish and macroinvertebrates. Diatoms have been shown to be useful indicators of changes in water quality resulting from pollution and land-use impacts.

Objectives: To determine the applicability of diatoms for hind-casting water quality in the KNP and to compare recent diatom community composition with those from the 1980s.

Methods: In this study, pH and electrical conductivity (EC) were used to evaluate temporal changes in water quality of three rivers within the KNP. Additionally, we made use of historic diatom samples from three of the five perennial rivers to evaluate if diatom communities reflected changes in water conditions between 1983 and 2015.

Results: Diatom community structure was significantly different between 1983 and 2015. Diatom-based index scores (SPI) indicated an improvement in water quality for the Letaba and Olifants rivers.

Conclusion: Diatoms were shown to be useful indicators of current water quality and are also useful for determining temporal changes.

Introduction

Rivers are invaluable infrastructure globally. They are the main sources of available surface water in many countries including South Africa. Less than 0.3% of all the available surface water is freshwater (Griffiths et al. 2015). This portion of water is reported to be on a decline both in quality and quantity (Pillay & Buckley 2001; Roux & Nel 2012; Laine et al. 2014). Various freshwater taxonomic groups such as diatoms, macroinvertebrates and fish are commonly used to monitor freshwater water quality (Taylor et al. 2007a; Boix et al. 2010; Bere & Mangadze 2014; Mangadze et al. 2016).

Five perennial rivers flow through the Kruger National Park (KNP) and although the KNP is a protected area, its rivers are not exempt from anthropogenically induced impacts that compromise water quality and flow (Dallas & Day 2004; Pollard et al. 2011). As a result there has been a steady decline in water quality of most rivers in the KNP over time (Pollard & du Toit 2011). The main anthropogenic activities impacting water quality are point source and diffuse pollution (Roux & Nel 2012; Barnard et al. 2021). Sedimentation of river beds resulting from overgrazing, agriculture and sand-mining also impacts water quality and ecosystem health (Dallas & Day 2004). River flow is mainly impacted by impoundment and abstraction (O'Keeffe & Davies 1991; Riddell et al. 2013). Agricultural, urban and industrial activities are commonly sustained by water extracted from rivers – approximately 60% of river water supports agricultural activities, 24% goes to domestic use in urban areas and 3% of the water is used for industrial activities (DWA 2013). Water quality and quantity are crucial for sustainable freshwater ecosystems to benefit both livelihoods and the environment. Additionally, water quality is a key driver of productivity in aquatic systems – for instance if a system becomes moderately nutrient enriched, increased productivity may support several organisms depending on photosynthetic organisms. In some instances, when primary productivity is high (eutrophication), this may lead to problems such as algae blooms with associated toxic effects and trophic disruptions (Dallas & Day 2004; Hart 2006, Tsu-Chuan & Clark 2018; Zheng et al. 2019).

An ideal water quality monitoring tool needs to be simple, quick, repeatable and preferably use aquatic organisms that are not seasonal and habitat dependent (Round 1991; De la Rey et al. 2004, Harding et al. 2005). Measures of river water quality in South Africa have conventionally been based on water chemistry as well as taxonomically different ecological indicator groups, such as fish and macroinvertebrates (De la Rey et al. 2004; Harding et al. 2004; Wepener 2008). However, water chemistry measurements are often expensive and only measure absolute values of a limited number of variables on the day of sampling (de la Rey et al. 2004), meaning that some water quality disturbances may be missed. Biotic responders, such as macroinvertebrates, can also be limiting because they have different life stages often linked to seasons (Round 1991) and their distribution is usually variable due to habitat and flow conditions (De la Rey et al. 2004). Other concerns are that they were developed for specific types of streams, usually wade-able, low flow streams, meaning they cannot be monitored during the high flow season (Bate et al. 2004; Harding et al. 2005).

Unlike other taxonomic groups regularly used for biomonitoring, diatoms are less dependent on seasons (no larval stages), flow and habitat (Round 1991; De la Rey et al. 2004). Diatoms are in the Class Bacillariophyceae and are unique among algae as they have a cell wall composed of amorphous biogenic silica. Diatoms are photosynthetic, reproduce rapidly and may be attached or locally motile. Diatoms form thick biofilms in South Africa during the winter months and are major contributors to primary production. Diatoms are extremely useful ecological indicators (De la Rey 2004; Bate et al. 2004; Harding et al. 2005; Harding & Taylor 2014; Mangadze et al. 2015; Dalu & Froneman 2016). Additionally, diatoms are not geographically limited and their distribution is chiefly driven by water quality. Furthermore, diatoms' short life span and fast reproduction (Rott 1991) allow them to respond rapidly when water quality changes. The siliceous cell walls do not easily deteriorate after sampling, which allows for long-term storage and analysis of specimens (Harding & Taylor 2011). Thus, diatoms have the potential to augment the current water quality monitoring methods.

In the past three decades (1983 to 2015), the KNP substantially influenced water management practices outside of the park. Adaptive management was implemented by KNP and external stakeholders, allowing real-time monitoring data to inform dam management and releases (Venter & Deacon 1995; McLoughlin et al. 2011; Pollard et al. 2011). Some of the management strategies implemented includes the new water act, compulsory licencing and formation of catchment management agencies to provide local monitoring, enforcement and water licencing. On closing the adaptive management loop, the real-time responses worked much better with flow, a more complicated but tractable system responder than quality, a more sluggish and complex system responder (McLoughlin et al. 2011; Pollard et al. 2011; Riddell et al. 2013). This ultimately led to all rivers flowing during the 2015–2017 drought, one of the most severe droughts recorded, both in terms of MAR (mean annual rainfall) and average temperatures (Swemmer et al. 2018). Maintaining river flow generally means increased dilution capacity and therefore improvement in water quality, which in the case of the present study would be reflected by diatoms.

In the present study we investigated river eco-status of three perennial rivers of the KNP to evaluate if diatom communities changed when river eco-status changed. This is a necessary step towards integrating diatoms into river eco-status monitoring programmes as a possible diagnostic tool for assessing water quality in future, specifically in the KNP. Additionally, we made use of water quality data to evaluate change in all major KNP rivers from 1983 to 2015. We used pH and EC to evaluate changes in water conditions at our sample sites because both variables were consistently collected. We then evaluated the potential of diatoms as water quality indicators by studying changes in diatom community structure in relation to EC and pH. We specifically made use of a customised version of the Specific Pollution sensitivity Index (SPI), also referred to as the South African Diatom Index (SADI).

Materials and Methods

Study area

The study was conducted in three perennial rivers, the Letaba, Olifants and Sabie rivers (Figure 1), flowing through the semi-arid region of the Kruger National Park (KNP), South Africa. This part of the KNP receives approximately 537 mm average annual rainfall. The perennial rivers experience variable seasonal flow regimes and

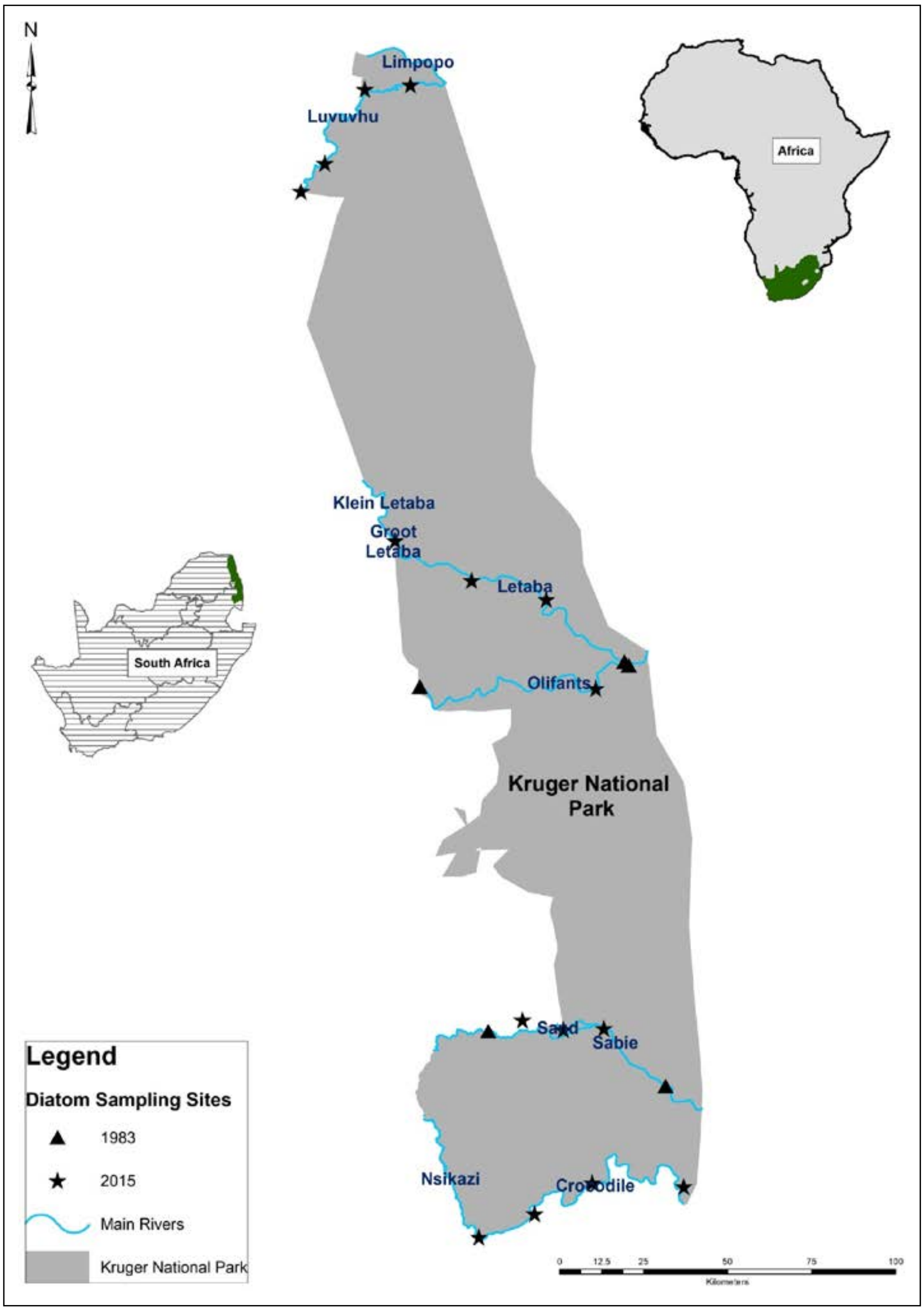

Figure 1. A map of the Kruger National Park, showing the location of the study area and diatom sampling sites.

are influenced by large infrequent disturbances such as floods and droughts (O'Keefee & Rogers 2003). The Olifants, Letaba and Sabie rivers have different catchment sizes and origins. The Olifants originates in the Highveld, far from the KNP. The Letaba and Sabie river originate close to the KNP and flow over similar geology (O'Keefee & Rogers 2003). Land-use activities along the Olifants catchment are mainly mining, agriculture and forestry. However, land-use activities along the Letaba and Sabie rivers include agriculture and forestry. The catchment length for the Olifants, Letaba and Sabie are 840 km, 573 km and 189 km respectively. A relatively long stretch of the Olifants and Letaba rivers are outside the KNP, accounting for 89% and 82% river length respectively. The Sabie River has only 37% of the river length outside the KNP (O'Keefee & Rogers 2003; Pollard et al. 2011). The present study compared samples collected in September 2015 to historical samples collected in March 1983, river flow is often stable in both months. The average rainfall for March 1983 was 1.39 mm and 1 mm for September 2015 (SANParks data).

Data collection

Diatoms

Diatom samples were collected in 2015 in the KNP by SANParks staff members. No chordates or vertebrates were collected during the study. All historic diatom samples used in this study are part of the South African National Diatom Collection (SANDC) housed at the

North-West University in Potchefstroom. These samples were collected in March 1983, using a similar sampling and slide preparation techniques as those used in the present study. Diatom samples collected in September 2015 followed the collection, preservation, preparation and analysis protocols as described in Taylor et al. (2007b). Briefly, five to ten average sized rocks (15 to 30 cm) were randomly selected. The selected rocks were located at least a meter away from the river bank in the flowing part of the river, to avoid isolated waters and eddies. The surface of the rocks was scrubbed with a small brush and the resulting suspension preserved with ethanol (> 20% final concentration). Samples were allowed to settle for 24 hours and then processed using the hot acid and $KMnO_4$ method (Taylor et al. 2007b). Slides were mounted in Pleurax (Taylor et al. 2007b). Diatoms were viewed using an Olympus BX41 light microscope and identified according to Taylor et al. (2007a).

Water quality

Physicochemical parameters measured in situ during 2015 included pH and EC (μS/cm). Measurements were recorded from active channels of the river before diatom samples were collected. A WTW LF95 (Weilheim, Germany) handheld water quality meter was used to measure EC and a Cyberscan pH 300 meter (Eutech Instruments) to measure pH. Unlike the diatom samples, historic physicochemical measurements included each year and all major rivers from 1983 to 2015. These historic physicochemical measurements were collated from the Department of Water and Sanitation official website (http://www.dwaf.gov.za/iwqs/wms/data/accessed 06/07/2018).

Data analysis

OMNIDIA ver. 5.3 diatom interpretative software was primarily used to generate index scores using the counted and identified cells (Lecointe et al. 1993). A value between 1 and 20 was allocated to each sample based on species sensitivity values (Lecointe et al. 1993; Harding & Taylor 2011) and then translated to an ecological class as shown in Table 1. The top five dominant species per river for the time periods were considered to elucidate drivers to specific water quality changes. Student t-tests were used to assess physicochemical parameters over time and their relationship to SPI score. An ANOSIM was also performed to test whether there were significant differences in diatom species similarity between years and a two dimensional multi-dimensional scaling (MDS) approach was used to visualise the similarity between sites using Primer 5 ver. 5.2.3 (Clarke & Warwick 2001)

Results

Changes in water quality indicators in the three studied rivers

The pH and EC varied considerably (pH: 6.3–8.9 and EC: 9.22–205.08) over time in all three studied rivers (Figure 2). The pH remained relatively similar ($p>0.05$) in the Olifants River over time, however for EC, there were significant differences ($P = 0.0013$) between 1983 and 2015 (Table 2). From additional historical data we also observed a steady decline in EC until early 2000, but it then stabilised at less than 90 μS/m from early 2000 to 2015 (Figure 2D). The Letaba River maintained an alkaline water column throughout 1983 to 2015. The EC was also generally maintained below 140 μS/m. The Sabie River reflected a more neutral water column from the early 1980s to an alkaline level in 2015. The Sabie River became more alkaline over time, with a significantly high pH in 2015 compared to 1983 ($P = 0.0004$). Although the EC was quite low during the study period (<50 μS/m), it doubled between 1983 and 2015 ($P = 0.0001$).

Diatom communities in 1983 and 2015

A two dimensional multi-dimensional scaling approach was used to visualise the similarity between sights and shows two different clusters, namely the 1983 and 2015 sites, indicating change over time (Figure 3). An ANOSIM was also performed to test whether there are significant differences in diatom species similarity between years ($P = 0.2$) and the R statistic of 0.587. Even though the p-value does not indicate a significant difference as the R value is closer to 1, it indicates that there are greater differences between the years than within the years. The MDS indicates two distinct year groups so the insignificant p-value obtained in the ANOSIM may

Table 1. Ecological Class values for diatom indices (Eloranta & Soininen 2002)

Ecological Class	Class	Trophy	Index Score (SPI/SADI)
A	High quality	Oligotrophic	>17
B	Good quality	Oligo-mesotrophic	15–17
C	Moderate Quality	Mesotrophic	12–15
D	Poor quality	Meso-eutrophic	9–12
E	Bad quality	Eutrophic	<9

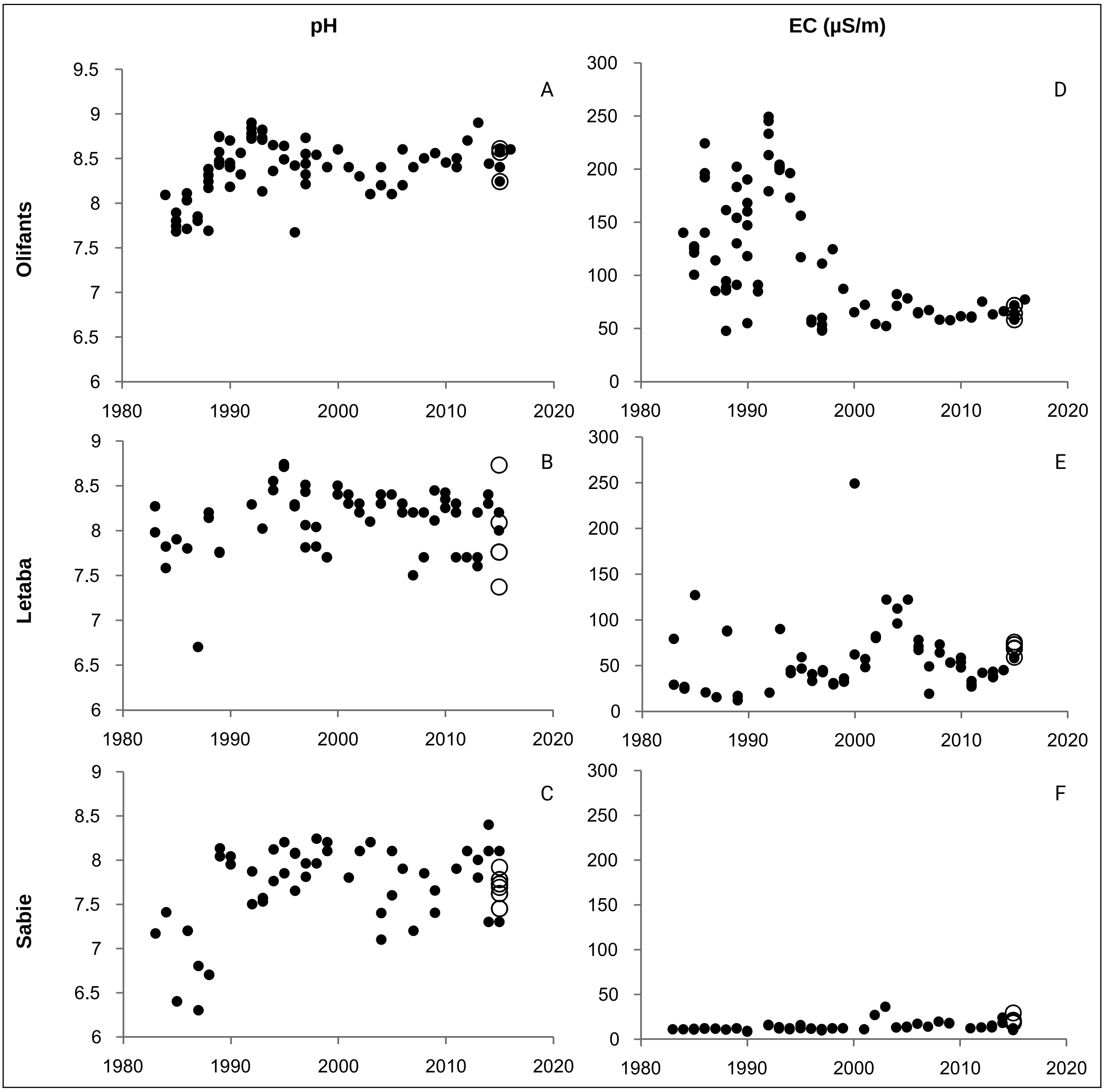

Figure 2. Long-term changes in two selected river chemical parameters in the Olifants, Letaba and Sabie rivers between 1983 and 2015. The closed symbols represent data extracted from the Department of Water Affairs and Sanitation. Open symbols represent the values recorded at sites within the three focal rivers during the present study in 2015.

be attributed to the small sample size and large number of different species collected.

The top five dominant diatom species in 1983 and 2015

The top five dominant diatom species at each site in 1983 and 2015 were compared in a table format (Table 4). Diatom species with more than 50% count were considered to be dominant. *Nitzschia frustulum* was dominant along the Olifants River in 1983. However, *Rhoicosphenia abbreviata* and *Epithemia sorex* became the two dominant species at 69.5% and 52.5% dominance respectively by 2015. *Rhopalodia gibba* dominated the Letaba River in 1983, but it decreased from 65.6% to 4% dominance in 2015, whilst *Gomphonema parvulum* reflected 66.5% dominance in the same year. The Sabie River was dominated by *Cymbella kolbei*. However, *C. kolbei* decreased from 79.5% dominance in 1983 to 5.25% dominance in 2015. *Encyonopsis leei* was the dominant species in 2015 for the Sabie River.

The SPI index association with two water quality variables

Both Olifants and Letaba rivers were eutrophic (Table 1) in 1983, reflected by a low SPI score of 7.4 and 7.1 respectively (Table 3). However, both rivers improved

Table 2. Mean pH and EC (μS/m) values in 1983 and 2015 across the three rivers. Values in brackets represent 95% confidence limits. We also provide the sample size as well as the results of t-tests comparing 1983 and 2015. Shaded blocks highlight significant differences

River	pH			EC (μS/m)		
	1983	**2015**	**t-test**	**1983**	**2015**	**t-test**
Olifants	8.14 (8.03-8.25) n=5	8.49 (8.15-8.83) n=4	t=3.89 df=3 p=0.03	149 (94.87-205.08) n=5	66.3 (53.64-78.95) n=4	t=6.44 df=5 p=0.001
Letaba	7.80 (6.77-8.82) n=4	7.87 (7.15-8.5) n=9	t=0.25 df=4 p=0.115	40.35 (11.96-92.67) n=4	69.93 (60.60-79.26) n=9	t=2.2 df=3 p=0.8
Sabie	7.16 (7.12-7.38) n=3	7.69 (7.38-8.00) n=6	t=8.25 df=6 p<0.001	11.60 (9.22-13.97) n=3	21.25 (13.25-29.25) n=6	t=5.34 df=6 p=0.001

in SPI score in 2015. Olifants doubled its SPI score to 14.8 and Letaba increased to 10.4. The Sabie River reflected oligotrophic (Table 1) water quality for both 1983 and 2015. SPI score was 18.9 and 18.8 (Table 3). There was an association between SPI score and EC. However, there was no relation between SPI score and pH (Figure 4). Rivers with large catchments outside a protected area are exposed to various land use practices that compromise the rivers' water quality.

Discussion

Diatom based observations reflected a general change in diatom species composition over time. A change in diatom species composition suggests that there has been a change in water quality along the Olifants, Letaba and Sabie rivers between 1983 and 2015 (Figure 3). Both the Olifants and Letaba rivers improved in water quality as was reflected by the diatom index (SPI score). However, the Sabie River did not show any significant change in water quality in relation to SPI scores.

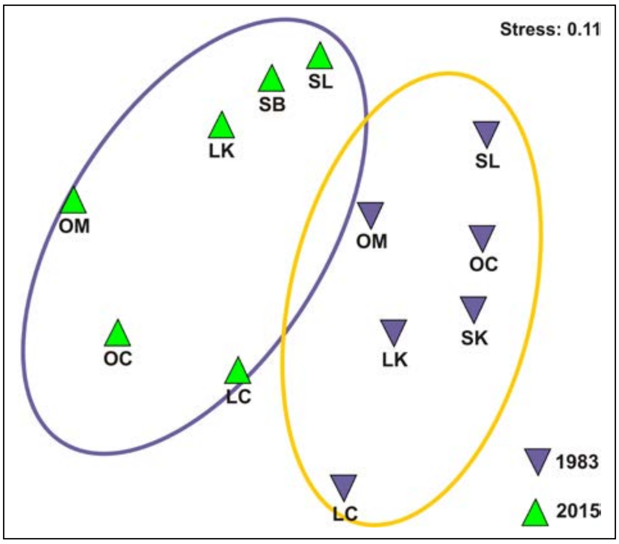

Figure 3. Two-dimension MDS plot of diatom community composition in 1983 and 2015 at different sites along the Olifants (OM and OC), Letaba (LC and LK) and Sabie rivers (SL and SB). Note that all sites' diatom composition shifted significantly from 1983 to 2015 irrespective of whether the index values changed or not (see Table 4). Sample site abbreviations also in Table 4.

O'Keeffe & Rogers (2003) suggest that the Sabie and Letaba rivers should have similar water quality considering the geology of their catchments. However, rivers are complex systems influenced by many aspects other than the geology (Stevenson & Pan 1999). The Letaba River has a significant proportion of its catchment outside the KNP. However, a significant proportion of the Sabie River catchment is within the KNP (Pollard et al. 2011), hence the Sabie River is considered the least modified river in the KNP, while the Letaba River is modified and impacted by impoundments and other anthropogenic activities (O'Keeffe & Rogers 2003). Impoundments often have severe consequences for water quality including dissolved oxygen reduction, increased carbon dioxide and increased EC (Dallas & Day 2004). Over and above the dams outside the KNP, the Letaba River has two impoundments located within the KNP, the Mingerhout and Engelhardt dams. These impoundments coupled with agricultural runoff and urban runoff (Dalu et al. 2015; Mangadze et al. 2017) could be compromising water quality in the Letaba River. However,

Table 3. Summary of river ecological class, SPI value and water quality status comparison of the Olifants, Letaba and Sabie rivers using diatom based observations for 1983 and 2015

River	1983	2015	Trophy
Olifants	SPI = 7.4 Eutrophic	SPI = 14.8 Meso-eutrophic	Meso-eutrophic
Letaba	SPI = 7.1 Eutrophic	SPI = 10.4 Meso-eutrophic	Meso-eutrophic
Sabie	SPI = 18.9 Oligotrophic	SPI = 18.8 Oligotrophic	Oligotrophic

Table 4. Comparison of top five dominant diatom species at each site in 1983 and 2015. Note that some diatom species with more than 50% (bold) dominance in 1983 were no longer dominant in 2015. In 2015 some of the dominant species were replaced by other species with more than 50% (bold) dominance

1983				**2015**		
Site name	**Species name**	**Count**	**%**	**Species name**	**Count**	**%**
Olifants River (OM)	*Nitzschia frustulum*	188	47	*Rhoicosphenia abbreviata*	278	69.5
	Navicula cryptotenelloides	84	21	*Cocconeis pediculus*	59	14.75
	Gomphonema parvulum	81	20.25	*Nitzschia frustulum*	41	10.25
	Seminavis strigosa	21	5.25	*Cocconeis placentula*	19	4.75
	Nitzschia kurzii	7	1.75	*Gomphonema pseudoaugur*	3	0.75
Olifants River (OC)	***Nitzschia frustulum***	**266**	**66.5**	***Epithemia sorex***	**210**	**52.5**
	Cyclotella meneghiniana	63	15.75	*Cocconeis placentula*	159	39.75
	Navicula cryptotenelloides	26	6.5	*Rhoicosphenia abbreviata*	13	3.25
	Gomphonema parvulum	13	3.25	*Nitzschia elegantula*	8	2
	Eolimna subminuscula	9	2.25	*Rhopalodia gibba*	5	1.25
Letaba River (LK)	*Pseudostaurosira brevistriata*	112	28	*Gomphonema parvulum*	91	22.75
	Nitzschia palea	101	25.25	*Nitzschia frustulum*	76	19
	Nitzschia frustulum	34	8.5	*Nitzschia paleacea*	45	11.25
	Navicula symmetrica	28	7	*Bacillaria paradoxa*	45	11.25
	Nitzschia umbonata	27	6.75	*Amphora strigosa*	38	9.5
Letaba River (LC)	***Rhopalodia gibba***	**67**	**65.699**	***Cocconeis placentula***	**266**	**66.5**
	Navicula symmetrica	13	.80	*Nitzschia palea*	25	6.25
	Navicula cryptotenelloides	5	12.75	*Nitzschia communis*	24	6
	Rhopalodia gibberula	4	4.90	*Epithemia sorex*	22	5.5
	Fallacia umpatica	3	3.92	*Rhopalodia gibba*	16	4
Sabie River (SB)	***Cymbella kolbei***	**318**	**79.50**	***Encyonopsis leei***	**215**	**53.75**
	Navicula rhynchocephala	31	7.75	*Gomphonema gracile*	35	8.75
	Navicula frustulum	15	3.75	*Achnanthidium affine*	33	8.25
	Gomphonema parvulum	7	1.75	*Navicula zanoni*	26	6.5
	Planothidium rostratum	5	1.25	*Cymbella kolbei*	21	5.25
Sabie River (SL)	*Planothidium rostratum*	199	49.75	*Encyonema leei*	168	42
	Staurosira elliptica	59	14.75	*Gomphonema parvulum*	54	13.5
	Anorthoneis dulcis	26	6.50	*Cymbella turgida*	44	11
	Navicula symmetrica	25	6.25	*Navicymbula pusilla*	43	10.75
	Navicula frustulum	25	6.25	*Sellaphora pupula*	20	5

all impoundments on the Sabie catchment are located outside the KNP. Although the Sabie River is considered to be the least modified of the two, our study has reflected significant changes in both EC and pH between 1983 and 2015. At the same time, there was a shift in diatom community structure between 1983 and 2015 (Figure 3), although there was no significant change in SPI score (Table 3).

The Letaba River experienced periodic lentification from the 1960s to mid-1990s due to impoundments for agriculture (O'Keeffe & Uys 1998; Pollard et al. 2011). However, flow was restored after negotiations between KNP freshwater management and catchment managers (O'Keeffe & Rogers 2003). We would expect dissolved salts to be more concentrated during this period, resulting from low flows and sometimes lentification and

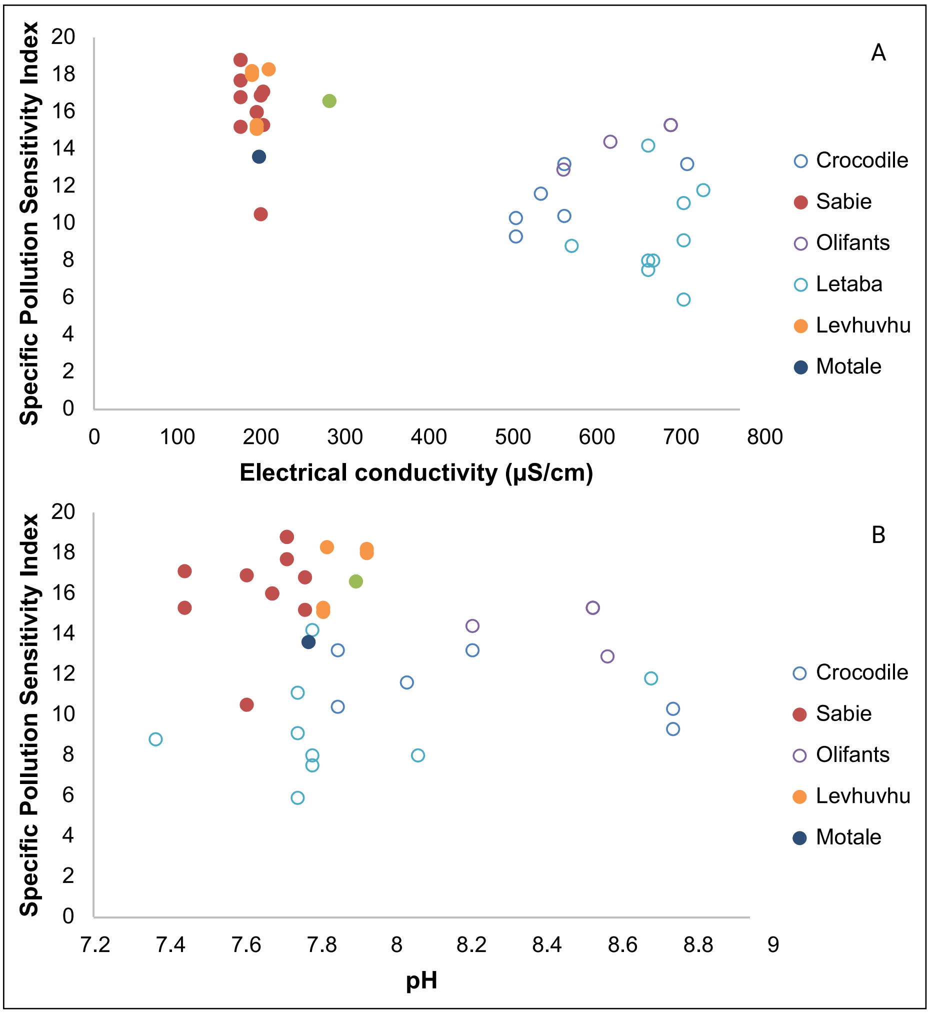

Figure 4. The relationship between SPI and two physicochemical water quality parameters. Open symbols represent rivers with large catchments outside the KNP. Closed represent rivers with relatively small parts of their catchments outside the KNP. In both cases, the darker the symbol, the larger the catchment.

subsequent higher evaporation rates. Our results did not show a significant increase in EC or a change in pH during the period (Figure 2) of the study, however, diatom based observations, however suggest that the Letaba River has improved in water quality between the two study periods. SPI scores increased from 7.1 in 1983 to 10.4 in 2015 (Table 3), which indicates the negative effects of these past processes.

Other than having a big catchment outside the KNP, the Olifants River is distinguished by its historic water quality problems emanating from agriculture, impoundments, abstraction and mining (Matlou et al. 2017). The observed high EC in the Olifants River may have resulted from sulphates and other pollutant input from mining (O'Keeffe & Rogers, 2003). We observed high dissolved salt concentrations between 1983 and early 1990s (Figure 2) in the Olifants River, more than five times the salt concentration in the Sabie River during the same period. An evident decrease in salt concentration occurred after the year 2000 (Figure 2). The decrease in salt concentration after 2000 could be due to Foskor mine losing its discharging licence under the new compulsory licencing imposed by the new Water Act of 1998 (McLoughlin et al. 2011). This halted discharge into the Selati River, a tributary of the Olifants River. The year 2000 flood event could also have diluted the salt concentration in the Olifants River. The KNP adopted the Strategic Adaptive Management plan for rivers in the late 1990s. This strategy promoted on-going evaluation and monitoring of the rivers followed by action to be taken against non-compliance (McLoughlin et al. 2011; Pollard et al. 2011). The mitigation strategies applied by freshwater managers seem to have paid off for the Olifants River, considering the decrease in salt concentration after 1990. Additionally, diatom-based observations also suggest that the Olifants River water quality has improved. The SPI score dramatically increased from 7.4 to 14.8 between 1983 and 2015 (see Table 3).

Diatom community structure indicated that there is greater differences between 1983 and 2015 than within the years as the p-value does not indicate a significant difference (R value: 0.587) for all focal rivers (Figure 3) irrespective of whether EC and pH changed or not (Table 2), suggesting broad system changes associated with non-measured water quality parameters. Most, if not all diatom sites sampled in 1983, plotted closer to each other when visualised on the multidimensional scaling (MDS). This is indicative of similarities in diatom community structure. Similarly, diatom sample sites investigated in 2015 also ordinated close to each other (Figure 3), meaning that the 2015 diatom community structures are also similar between sites. Diatoms could also be responding to other water quality requirements such as nutrients, which are not accounted for in this study.

Bate et al. (2004) indicated that pH might not be a good proxy indicator for water quality and this is borne out in the present study. We also did not observe any relationship between SPI and pH measurements between rivers in 2015 (Figure 4B). However, we observed a significant negative association between SPI score and EC measurements between rivers (Figure 4A). The rivers with large catchments (Olifants, Crocodile and Letaba) generally had high EC and low SPI scores. However, the rivers with smaller catchments (Sabie, Levuvhu and Motale) had low EC and high SPI scores. The observed low EC and high SPI scores suggest that rivers with smaller catchments are in a better water quality status than rivers with large catchments. This observation suggests that protected areas minimise pollution input within their boundaries.

The sub-cosmopolitan concept of diatom distribution suggests that diatom species assemblages and diversity are not determined by geographical location (Round 1991; Smol & Stoermer 2010), but by water quality parameters (Round et al. 1991). In other words, diatom species thrive in an aquatic ecosystem that satisfies their environmental requirements. For example, diatom species tolerant to elevated nutrients will be abundant in a river system that has excess nitrogen and phosphorous (Hall & Smol 2010; Stevenson & Pan 1999). The Olifants River was dominated by *Nitzschia frustulum* species during 1983 (Table 4), reflecting high levels of pollution and brackish water. However, *Rhoicosphenia abbreviata* and *Epithemia sorex* became dominant in 2015, indicating moderate EC and elevated nutrient levels. In 1983 the Letaba River was dominated by *Rhopalodia gibba,* which was replaced by *Cocconeis placentula* in 2015 (Table 4). The change in diatom species dominance indicates that the Letaba had high EC waters in 1983 and meso-eutrophic water in 2015 (Table 3). The Sabie River was dominated by *Cymbella kolbei* species, which requires water quality at moderate to high EC. *C. kolbei* was replaced by *Encyonema leei* (Table 4), commonly occurring in slightly acidic and oligotrophic waters. This species, described from China, has recently been documented from many river systems in South Africa (unpublished data) with no historical records or depiction of it previously being present in the country. There is currently limited knowledge on the occurrence and ecological requirements of this species. Diatom samples collected in different years have reflected the water quality status of the sites at the time of sampling. Additionally, historically-curated diatom samples were also successfully used to hindcast historic water quality status for the KNP rivers.

Conclusion

The present study showed that EC values have changed over the decades as has the associated diatom community structure, reflected by SPI scores. The pH did not show a relationship with diatom community structure changes. The Olifants and Letaba rivers showed an improvement in water quality whilst the Sabie River remained approximately the same although the diatom community structure has changed. Additionally, we observed that rivers with small catchment sizes had better water quality conditions compared to rivers with large catchment sizes outside the KNP. The study suggests that diatom assessments might be a useful biomonitoring tool to assess health of rivers over time.

Authors' contributions

PS (SANParks/North-West University) was responsible for experimental and project design, field work and main author. JT (North-West University) was the supervisor for the project at NWU, contributed to data analysis and acted as second author. DG was the supervisor for the project at the Kruger National Park and contributed to the project design and final text. JB (SANParks) contributed to the statistical analysis and interpretation of the data as well as to the final text.

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Impact of land-use and flow conditions on the phytoplankton of the Sabie River, South Africa

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Background: The understanding of the impact of land-use on the dynamics of phytoplankton assemblages during varying climate conditions on rivers is limited.

Objective: To determine the impact of land-use types and flow on phytoplankton assemblages in the Sabie River.

Methods: The relationships between land-use patterns, water quality and phytoplankton assemblages were analysed using canonical correspondence analyses (CCA).

Results: Six main land-use types could be distinguished in the eight identified sub-catchments of the river. The CCA results showed that the land-use had a stronger correlation with phytoplankton classes during the higher flow conditions than during low flow conditions. The forestry land-use type had the strongest correlation with nitrate–nitrite concentrations in the Sabie River. Chlorophyll-*a* concentrations were higher during 2016, and a slightly lower number of genera were observed for the class Chlorophyceae. During 2017 the number of genera of the class Cyanophyceae decreased together with chlorophyll-*a* and total cell concentrations.

Conclusion: Low flow conditions favoured filamentous genera that are common to mesotrophic conditions while higher flow conditions favoured single-celled small genera more common to oligotrophic waters with higher disturbance. This study showed that flow has the potential to enhance the impact of land-use on phytoplankton community dynamics in a river system and thereby may have further impacts on the health and activities of surrounding communities.

Keywords: river, water quality, cyanobacteria, drought, phytoplankton biomass.

Introduction

Climate and land-use are two emerging factors (since 2006) that impact on and threaten freshwater biodiversity and aquatic ecosystem health (Hayes et al. 2015; Abirhire et al. 2016; Xizhi et al. 2017; Reid et al. 2019). Many studies have shown that land-use changes and pressure can significantly affect the water quality of rivers, lakes and reservoirs (Kändler et al. 2017; Vrebos et al. 2017; Shi et al. 2017). Agriculture and urbanisation can increase the transport of nutrients into water bodies via run-off (Xu & Zhang 2016; Shi et al. 2017), and therefore also influence phytoplankton abundance and composition (Katsiapi et al. 2012). The effect of climate is more difficult to quantify since precipitation and temperature affect the flow of water, whilst nutrient loading is known to alter phytoplankton assemblage, diversity and biomass (Michalak 2016; Bussi et al. 2016). Poor water quality and higher temperatures are often associated with high cyanobacterial biomass (Abirhire et al. 2016; Bussi et al. 2016), while the Chrysophyceae, Dinophyceae and Bacillariophyceae are often associated with lower nutrient levels (Katsiapi et al. 2012). The biodiversity and biomass of the Chrysophyceae are known to decrease as the Cyanophyceae cell concentrations increase (Katsiapi et al. 2012). Organic enrichment in rivers is known to favour Euglenophyceae (Katsiapi et al. 2012).

Despite the fact that freshwater ecosystems are hotspots for biodiversity endangerment (Reid et al. 2019), there still is a bias towards conserving terrestrial biodiversity (Cantonati et al. 2020). Freshwater biodiversity is particularly vulnerable as it is also a vital resource for humans (Cantonati et al. 2020). The use of freshwater ecosystem services will inevitably have a negative effect on water quality (Cantonati et al. 2020). Any change in the physical condition and nutrient inputs, which affect the dynamics of a phytoplankton community, can have far-reaching effects on the health and activities of those surrounding human communities due to nuisance bloom forming species (Winder & Sommer 2012).

The water quality of the Sabie River is regarded as relatively good when compared to other rivers in the Limpopo Province such as the Olifants and Crocodile rivers (Griffin, Palmer & Sherman 2014; Shikwambana et al. 2021). The water of the Sabie River system is very important to both the society and the regional economy, which relies heavily on agriculture and ecotourism (Tlou 2011; Roux et al. 2017). Commercial forestry plantations, commercial agricultural lands and urbanisation are having an increasing impact on the water demands in the catchment (Roux et al. 2017). This has the potential to negatively impact not only on the aquatic and riparian zones, but also on ecotourism in the conservation land-use areas. According to Roux et al. 2017, as well as field observations made during this study, pollutants enter the Sabie River and its tributaries through stormwater run-off drains and dumping of domestic waste in the rivers and riparian zones. Dysfunctional wastewater treatment works further contribute to a decline in water quality (Barnard et al. 2019). Rural and now peri-urbanising communities in the Bushbuckridge area greatly increased in extent due to rural migration and immigrants from neighbouring countries (Pollard & Walker 2000; Tlou 2011).

The water demands for this area are expected to increase, with a concomitant and magnifying impact on the water quality of the Sabie River's tributaries, such as the Marite, and the Sand, and ultimately impact on the Sabie River. Moreover, this is expected to impact on phytoplankton diversity and biomass. Monitoring the impact of anthropogenic disturbances on freshwater quality is essential to indicate the viability of the water source for the provision of various ecosystem services (Katsiapi et al. 2012). This has particular relevance during changing climatic conditions such as the drought experienced in the Sabie–Sand catchment during 2016 (Smit 2017) and the impacts of immediate postdrought periods of higher precipitation in 2017.

The aim of this study was two-fold, to investigate: (i) the impact of the current land-use (forestry, agriculture/settlements and conservation) on phytoplankton assemblages of the Sabie River during low flow conditions of a drought; and (ii) whether higher flow conditions immediately after the drought altered the impact of land-use and land cover. To meet these aims the first objective was to determine the land-use and land cover of the study area. The second objective was to determine the nutrient levels that support phytoplankton growth, and the third objective was to determine the change in phytoplankton assemblages in the Sabie River during low flow conditions followed by high flow conditions.

Materials and Methods

Study area

The Sabie–Sand Catchment is one of three sub-catchments that fall under the Inkomati–Usuthu Water Management Area (IUWMA). As seen in Figure 1, the Sabie–Sand Catchment lies in the north of the IUWMA, and the Kruger National Park (KNP) is situated to the east where the Sand River joins the Sabie River as one of its main tributaries (Pollard & Du Toit 2011). The Sabie River flows through three distinct land-use zones, namely: (i) a forestry-dominated mountainous area to the west; (ii) a hilly and undulating landscape dominated by dense settlements and smallholder farming; and (iii) a large conservation area including the KNP and the Sabie-Sands Game Reserve in the east. The Sabie River in Mozambique decants into Corumana Dam before finally entering the Incomati River near the town of Moamba in Southern Mozambique (Pollard & Du Toit 2011).

According to the vegetation classification by Mucina and Rutherford (2006), the upper Sabie Catchment is part of the Mesic Highveld Grassland Bioregion and the lower catchment, below Sabie, forms part of the Lowveld Bioregion. Each bioregion constitutes a number of more detailed vegetation types as described by Mucina and Rutherford (2006). Whereas the upper catchment is grassland, the lower catchment is savanna with a prominent woody layer and grass-dominated herbaceous layer. The average annual rainfall decreases along the topographical gradient from the mountainous areas in the west through the foothills and towards the lower, flatter reaches of the Sabie River in the east. Rainfall ranges from 900 to 1 500 mm/a in the west and 348–600 mm/a in the east of the catchment. Eight sampling locations were chosen in collaboration with the Incomati-Usuthu Catchment Management Agency (IUCMA) (Figure 1). These eight sampling sites were at the same localities where IUCMA sample from in order to make data sharing possible.

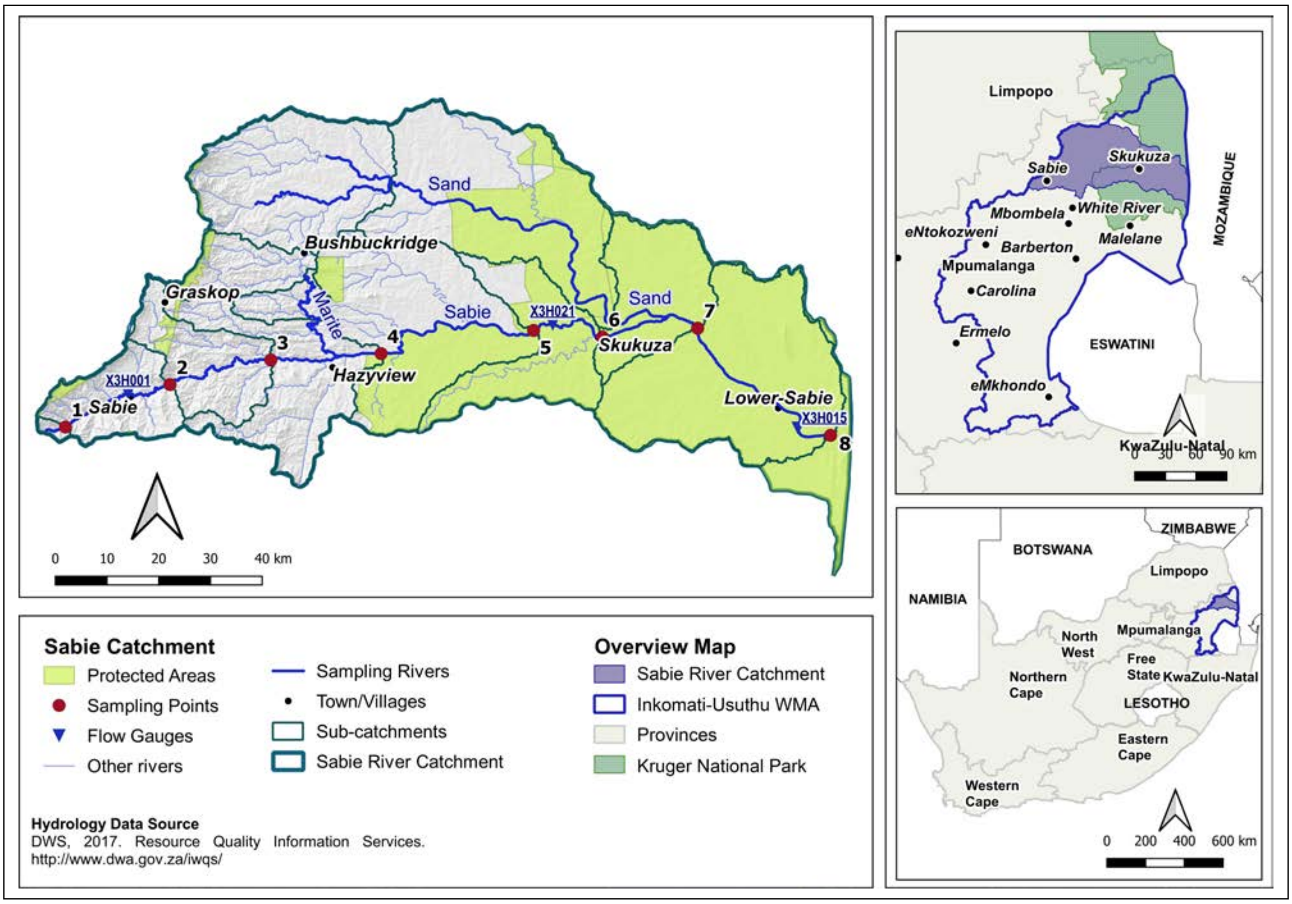


Figure 1. Locality map indicating the geographical position of the Sabie Catchment (insert) and the distribution of the eight sampling sites and the three gauge stations associated with the drainage basins.

Sample collection and analyses

Sampling of chemical and physical variables occurred on eight separate occasions, during January, April, July and October of 2016 and 2017. During each sampling occasion, a nine litre grab sample of surface water was taken at each sampling site. The physical-chemical parameters were determined *in situ,* using a YSI 556 handheld field multi-meter, that included: barometric pressure (mmHg); electrical conductivity (μS/cm); percentage dissolved oxygen (%DO); pH; and water temperature (°C). The multi-meter was calibrated by Rand Water Analytical Services before each sampling trip according to the manufacturer's prescribed protocol.

All chemical, microbiological and hydro-biological analyses were carried out by Rand Water Analytical Services. The standard methods of the American Public Health Association (APHA) (2013) were used, and the laboratory is accredited according to the South African National Accreditation System (SANAS) that is affiliated to the International Laboratory Accreditation Cooperation (ILAC). Due to the method of detection used and the reporting limit set by Rand Water, it was decided to report the concentration of total phosphates. The reporting limit for ammonia at Rand Water is <0.05 mg/l and values reported here for ammonia (NH_3) are derived from the measured ammonium (NH_4^+). Dissolved inorganic nitrogen is calculated as the sum of the concentrations of $NH_3 + NO_3^- + NO_2^-$.

Samples for phytoplankton identification and enumeration (250 ml) were preserved on-site with formaldehyde (2%). Planktonic phytoplankton cell identification and enumeration were done at the North-West University using the sedimentation technique according to Swanepoel et al. (2008).

Flow data for the study area were obtained from the IUCMA as a daily average flow rate in cubic metres per second from the following gauge stations with their respective Department of Water and Sanitation codes: Sabie (X3H001), downstream of Site 1, Kruger Gate (X3H021), close to Skukuza town between sites 5 and 6, and Lower Sabie (X3H015), between sites 7 and 8 (Figure 1).

Spatial analysis

Drainage basins were derived for each sampling point based on the 30 m Shuttle Radar Topography Mission (SRTM) digital terrain model (NASA JPL, 2013) as input using the drainage tool as part of ESRI Spatial Analyst

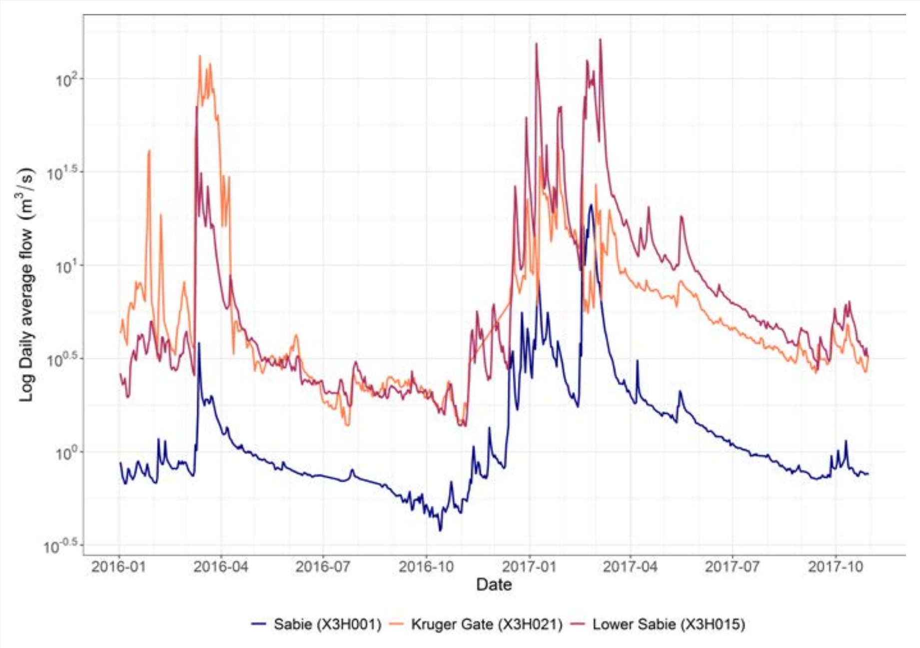


Figure 2. Flow data for the Sabie River for 2016 and 2017 recorded at the different gauge stations located in the study area.

extension (ESRI, 2019). Land-use data were derived using the 72 class 2014 Land Cover data (GEOTERRA IMAGE, 2015) in combination with the 2016 protected area data provided by the Department of Environment Affairs (DEA 2016). The 72 class 2014 land cover datasets were reclassified into five broad land cover classes (water, natural vegetation, cultivation, plantations, urban and mines). The natural vegetation class were thereafter split into grazing and conservation land-uses based on the DEA protected area layer. Using an R script, the frequency distribution of land-use classes was estimated for each drainage basin areas using the Raster and SF packages. The percentage distribution of each class was used as input to the Canonical Correspondence Analysis (CCA).

Statistical analysis

The water quality dataset consisted of biological, chemical and physical parameters. Results that were below the reporting limit were assigned a value of half the reporting value in order to be included in the statistical data sets. Missing data were treated as gaps, and 0 was used where the variable was measured as zero. All statistical analyses were carried out using Statistica v13, Dell Inc. (2016). Initially, the Kolmogorov-Smirnov and Lilliefors tests for normality were conducted to determine if the data were distributed parametrically. The data did not meet the assumptions of normality in the distribution of all variables and thus non-parametric statistics were applied. Kruskal-Wallis analysis (comparison of multiple groups) was used to compare multiple independent groups, along with Spearman's rank correlation coefficient. Data that were below the limit of detection were substituted with half the value of the detection limit provided that it came to no more than 50% of the data. If 100% of the data were below the detection limit it was specified.

Canonical Correspondence Analysis (CCA) was performed using Canoco v4.5 (Ter Braak & Šmilauer 2002). The CCA was used to determine if land-use/cover and water quality had a statistically significant relationship with phytoplankton assemblages of the Sabie River. It was conducted for both 2016 and 2017. Log transformation of the datasets, that is, log(y+1) was applied. A Monte Carlo permutation test (499 permutations) was used to determine the statistical validity of the CCAs.

Results

Hydrological flow conditions

The hydrograph (Figure 2) shows that average daily flows during 2016 were significantly ($p < 0.05$) lower than during 2017, especially at the lower Sabie gauge (close to Site 7). Although high flows were experienced during the rainfall season of both years at the Kruger Gate gauge station, average flows were higher and more consistent at all three gauge stations throughout 2017.

Land-use

Six main land-use types could be distinguished in the eight identified sub-catchments of the river. The distribution of land-use and land cover can be seen in Table 1 and Figure 3.

Sub-catchments 1 and 3 are dominantly used for plantation forestry. Land-use of sub-catchments 4 and 5

Table 1. The percentage (%) land-use in each of the sub-catchments during 2016 and 2017

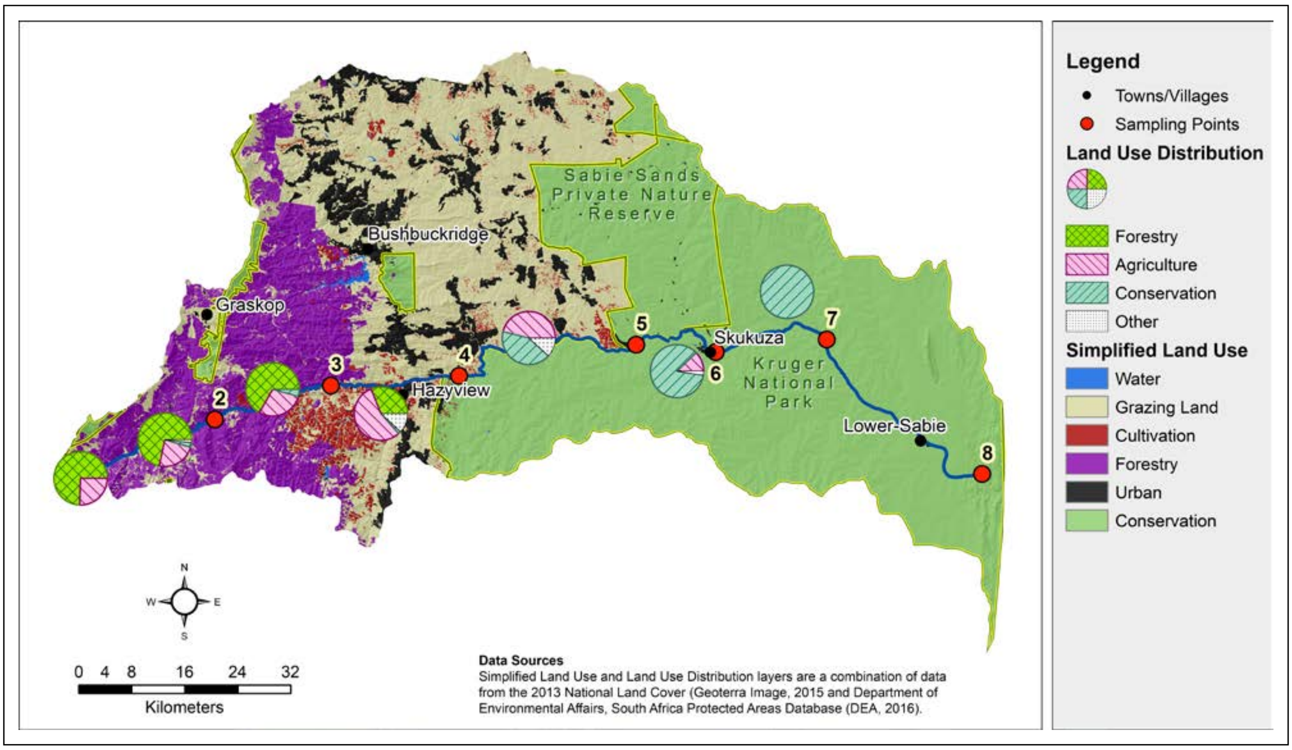
	Area	**Forestry**	**Agriculture**		**Other**		**Conservation**
Site	ha	Plantations	Cultivation	Grazing Land	Urban	Water	Conservation
1	1700	74.4	1.2	24.3	0	0	0.1
2	30432	71.6	0.2	23.6	1.7	0	2.9
3	35513	66.2	8.9	19.7	0.7	0.2	4.3
4	53767	31.1	13.5	42	11.2	0.5	1.7
5	87847	0.1	3.1	43	11.6	0.1	42.2
6	46220	0	0.4	11.8	2.4	0.1	85.3
7	43191	0	0	0	0	0.1	99.9
8	105845	0	0	0	0	0.1	99.9

is a combination of grazing land, plantation forestry, cultivation and rural settlements classified as urban. Sub-catchment 6 is predominantly natural vegetation under conservation as well as a small percentage of natural vegetation used as grazing land. The sub-catchments associated with sampling sites 7 and 8 are located within the KNP and therefore a natural landscape.

Plantation forestry is predominantly eucalyptus and pine, whilst intensive, irrigated sub-tropical fruit and nut orchards exist in the western cultivated area. Dryland grain and winter irrigated vegetable production is typical of the eastern region adjacent to the conservation areas. The grazing land is mostly used for subsistence and communal livestock production.

Spatial and temporal changes in nutrient and chlorophyll concentrations

Figure 4 presents the average values ± the standard deviation of chlorophyll-a (chl-a) and that of the main nutrient concentrations that can impact on phytoplankton assemblages. The total phosphate concentrations decreased at most of the sites during 2017, except at



Data Sources
Simplified Land Use and Land Use Distribution layers are a combination of data from the 2013 National Land Cover (Geoterra Image, 2015 and Department of Environmental Affairs, South Africa Protected Areas Database (DEA, 2016).

Figure 3. Land-use distribution between natural grazing land, conservation, urban, plantations and cultivation for the sub-catchments surrounding the eight sampling sites within the Sabie River Catchment (Geoterra Image 2015; DEA 2016).

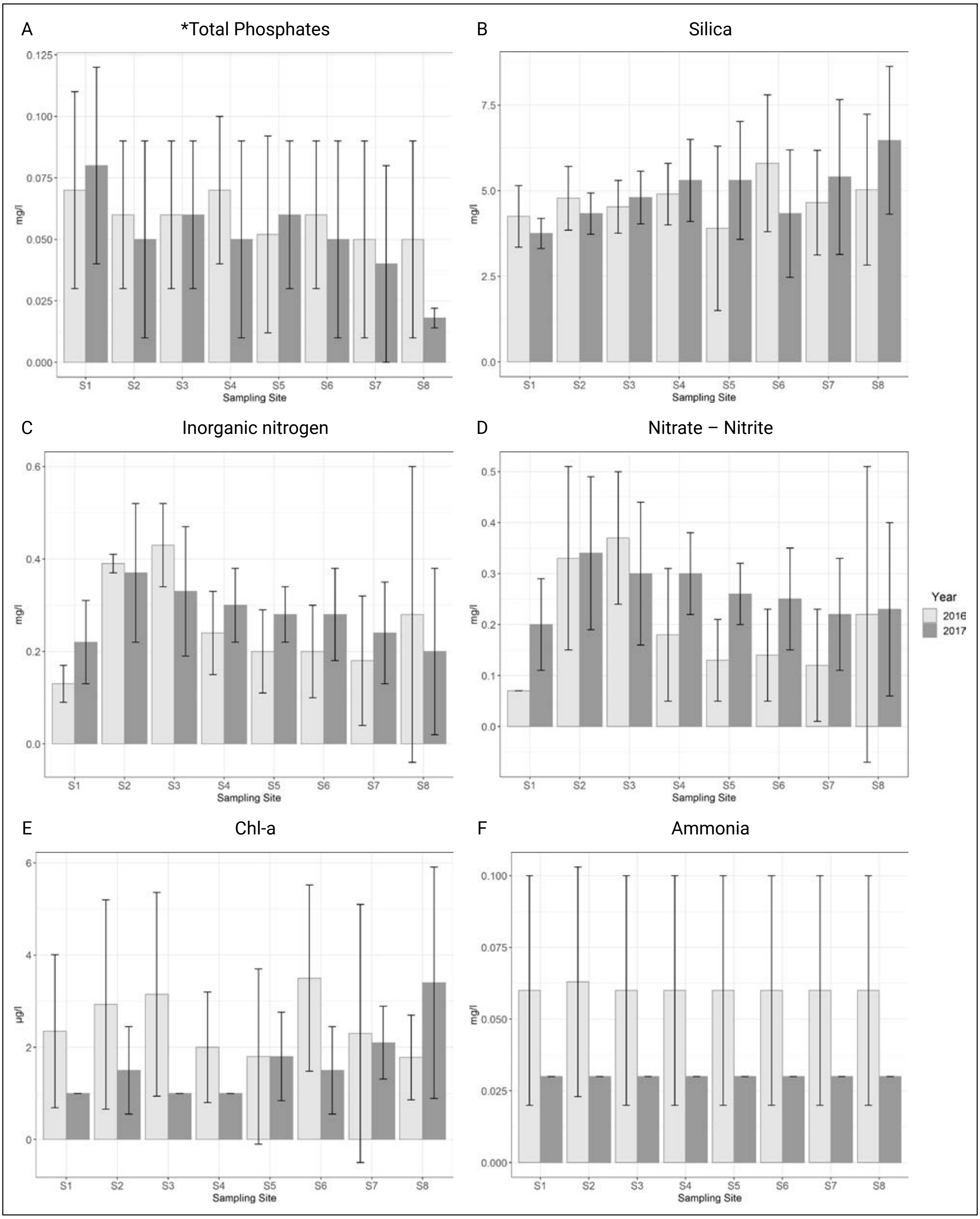


Figure 4. Average values ± standard deviation (n=4 for 2016 and for 2017) of the measured water quality parameters at sampling sites 1–8 for 2016 and 2017. Chl-*a*: Chlorophyll-*a*.

sites 1, 3 and 5 where it increased. The concentrations of silica increased during 2017, except at sites 1, 2 and 6. Silica concentrations appear to increase downstream as well during 2017 (Figure 4b). All concentrations determined for ammonia, during 2017, were below the reporting limit. The average concentration of dissolved inorganic nitrogen measured at all the sites during 2017 was <0.5 mg/l, which is indicative of oligotrophic conditions (DWAF 1996). This is also supported by the range of chlorophyll-a concentrations determined at all of the

Table 2. List of phytoplankton classes and number of genera observed for each class during 2016 and 2017

Phytoplankton class	2016	2017
Bacillariophyceae	20	20
Chlorophyceae	15	19
Cyanophyceae	13	12
Euglenophyceae	1	1
Dinophyceae	1	1
Chrysophyceae	1	1
Total genera	**51**	**54**

sites, which was consistently <10 µg/l. Sites 2 and 3 were the only sampling locations that showed a maximum concentration for inorganic nitrogen of >0.5 mg/l. The average inorganic nitrogen concentrations, however, increased during 2017 at most sites (except sites 2, 3 and 8), and this was mostly due to the increase in nitrite and nitrate during 2017 (Figure 4d), except at Site 3 where it decreased. Chlorophyll-*a* concentrations decreased at sites 1–4, and sites 6 and 7, while sites 5 and 8 experienced an increase in chl-*a* concentrations during 2017.

Phytoplankton biodiversity and abundances

Table 2 lists the six phytoplankton classes that were identified during both sampling years. The Bacillariophyceae were the most diverse group in 2016, with 20 genera followed by the Chlorophyceae with 15 genera. Thirteen Cyanophyceae genera were identified as well as one genus from each of the Euglenophyceae, Dinophyceae and Chrysophyceae, resulting in a total of 51 genera. During 2017 only the Cyanophyceae showed a decrease in biodiversity. The phytoplankton diversity was similar in 2017 with the identification of 20 genera from the Bacillariophyceae, 19 genera from the Chlorophyceae, 12 genera from the Cyanophyceae, and one genus each from the Euglenophyceae, Dinophyceae and Chrysophyceae, resulting in a total of 54 genera. Sites 7 and 8 exhibited the greatest diversity of genera for all the classes.

From the headwaters (Site 1) phytoplankton diversity increased downstream in the Sabie River to Site 8 during both the drought period (2016) and the immediate post-drought period (2017), while the total number of genera observed increased during 2017 (Table 2). Several genera were observed exclusively during the drought period, while others were observed only during the immediate post-drought period. These genera are listed in Table 3.

However, the total cell concentration of phytoplankton cells (cells/ml) in the catchment were higher in 2016 (2 090 cells/ml) than in 2017 (1 147 cells/ml). The most abundant class observed in the Sabie River was the Bacillariophyceae, and this was the dominant class in 2016 (Figure 5A) at all the sampling sites except Site 4, where the Cyanophyceae was the most abundant class. The most abundant class during 2017 (Figure 5B) was again the Bacillariophyceae, followed by the Chlorophyceae except at sites 6, 7 and 8 where the Cyanophyceae was the second most abundant class.

Impact of land-use on phytoplankton assemblages

The water quality of a water body can potentially be a reflection of the impact of the land-uses within the catchment as it receives precipitation and water flows though the landscape. Each sampling site also has a sub-catchment that can add to the influence of the antecedent water quality from upstream, which will impact phytoplankton biomass and composition.

To determine the impact of land-use on the phytoplankton assemblages of the Sabie River a CCA was conducted for both 2016 and 2017 (Figure 6A,B). This shows

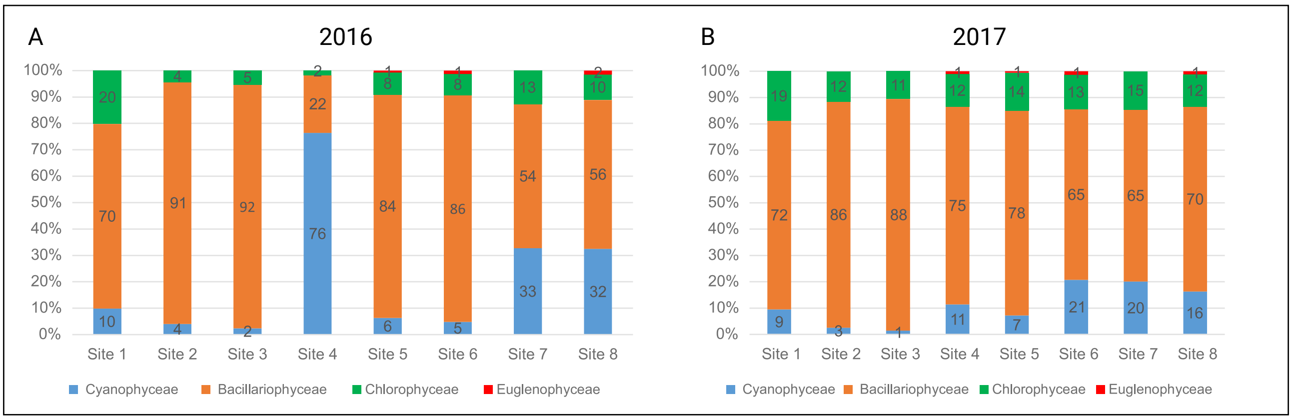


Figure 5. Percentage total abundance (cells/ml) of the different phytoplankton phyla at each of the sites observed during the four sampling occasions in 2016 (A) and 2017 (B).

Table 3. A summary of the genera of each phytoplankton class observed exclusively during the drought period (2016) and the immediate post-drought period (2017)

	Genera observed exclusively	
Phytoplankton class	**2016**	**2017**
Cyanophyceae	*Geitlerinema, Pseudanabaena, Snowella, Spirulina*	*Cylindrospermopsis, Gloeocapsa, Radiocystis, Synechocystis*
Bacillariophyceae	*Hippodonta, Rhopalodia*	*Frustulia, Hantzschia, Pinnularia, Planothidium, Urosolenia*
Chlorophyceae	*Closterium, Microspora, Mougeotia, Tetraedron*	*Cosmarium, Dictosphaerium, Kirchneriella, Ulothrix*
Euglenophyceae	*Phacus*	*Strombomonas*

that land-use had a statistically strong relationship with the phytoplankton assemblages in 2017 during immediate post-drought conditions, a year characterised by flash floods and high run-off in the study area (Figure 2). The first axis of the CCA explains 68.6% of the variance in the species–land-use relationship observed in 2016 ($p=0.668$) whereas this increased to 94.7% during 2017 ($p=0.144$). During 2017 forestry had the greatest influence on the data compared to conservation land-use type during 2016.

During both 2016 and 2017, the conservation and forestry land-use types could explain most of the variance in phytoplankton abundance. During 2016 sites 1–3, located in the forestry and agriculture land-use types, closely associated with higher ammonia, nitrate–nitrite and total phosphate concentrations together with the Bacillariophyceae and Chlorophyceae, and higher chlorophyll-a concentrations. Site 4 associated closely with the land-use type agriculture, total phosphates and the class Cyanophyceae, while the class Chrysophyceae associated closely with the land-use type ‘other’. The low concentration of Dinophyceae and Euglenophycea, and to a lesser extent the Chlorophyceae cells, associated strongly with the conservation land-use type. During 2017 sites 1–3 were closely associated with higher nutrient concentrations. A strong association between the Chrysophyceae and Site 3 was observed during 2017. Site 4 still associated with the land-use type agriculture and total phosphates, while Site 5 and the land-use type ‘other’ no longer associated with a particular phytoplankton class. Sites 7 and 8, in the conservation land-use type, associated closely with the class Cyanophyceae and Euglenophyceae, but no longer the Dinophyceae. The location of the Bacillariophyceae and Chlorophyceae so close to the origin of the axes of the ordination may indicate their ubiquitous distribution at all of the sites.

Discussion

The health of human societies and the ecosystems surrounding them is dependent on the quality and availability of freshwater. Unfortunately, human and land-use activities have exploited this resource heavily, and as a result, freshwater ecosystems are under threat (Cabecinha et al. 2016). Besides the impact of anthropogenic stressors, climate change has also been shown to threaten freshwater biodiversity and aquatic ecosystem health (Hayes et al. 2015; Abirhire et al. 2016; Xizhi et al. 2017; Reid et al. 2019). Results presented during this study have shown that both land-use and hydrological flow, can influence nutrient concentrations and abundance and dynamics of phytoplankton assemblages in the Sabie River.

Land-use affects water quality in two ways, one by the input of nutrients into the source water due to various activities and two by changing the land surface and therefore the surface run-off and input of nutrients and other elements such as heavy metals (Hayes et al. 2015; Xizhi et al. 2017). During 2017 river flow was persistently higher than 2016 even during the dry seasons. It has been reported that water quality has a stronger relationship with land-use during high flow than during low flow conditions (Shi et al. 2017), indicating that land-use has a greater influence on water quality during periods of high flow. This was also true during this study as was illustrated by the CCA (Figure 6B). During this study commercial agricultural areas and forestry land-use types could be associated with higher inorganic nitrogen concentrations in the Sabie River both 2016 and 2017 (Figure 6A,B). This was also found in other studies that showed during that high concentrations of nitrite–nitrate, ammonia and total phosphates in stream water could be linked to the use of fertilisers in agriculture (Shi et al. 2017; Xizhi et al. 2017).

The positive association of urban areas and inorganic nitrogen can be related to urban run-off and wastewater treatment plants (Namugize et al. 2018) such as that situated close to the river at Site 2. The average total phosphate concentration, however, decreased from 2016 to 2017 except at sites 1, 3 and 5, where it increased, probably due to agricultural activities and the use of fertilisers. Increases in both nitrite–nitrate and

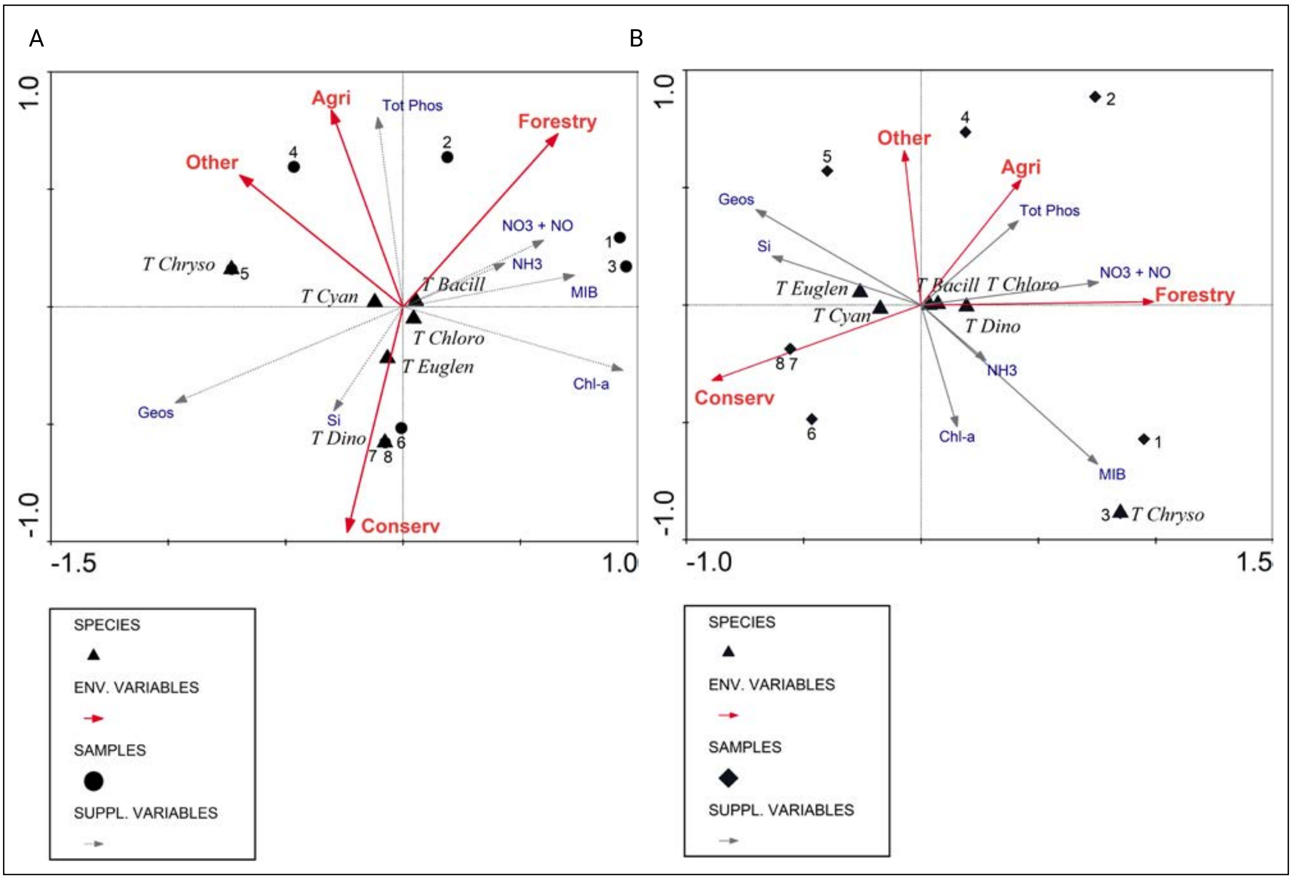


Figure 6. Triplot of the canonical correspondence analysis to determine the relationship between the land-use/land cover (env. variables) and phytoplankton classes (species) during (A) the dry period of 2016 and (B) for the immediate post-drought period of 2017. Water quality parameters were used as supplemental variables (Suppl.).

silica concentrations were observed at most sites during 2017. This can probably be ascribed to nutrients leaching from the soils during higher run-off. The overall decrease in ammonia concentrations observed during 2017 was most probably due to the flushing of effluent sources that caused the level of ammonia to increase during low flow/drier conditions. Chlorophyll-*a* (biomass) also decreased from 2016 to 2017 at most sites. This decrease can be the result of dilution due to higher flow, however other studies have also noted a decrease in biomass after periods of high precipitation (Stockwell et al. 2020). Chlorophyll-*a* concentration is a very clear indicator of nutrient changes and a responsive indicator of N and P concentrations and ratios (Gökçe 2016).

Water quality measurements only provide us with a snapshot of what the water quality is at the time of the measurement. On the other hand, phytoplankton abundance, dominance and community structure can more accurately reflect the water quality and impacts thereupon (Gökçe 2016). In the present study the most abundant group of algae in rivers was the Bacillariophyceae (Wher et al. 2015). The genera observed from this group are cosmopolitan and thrive in low flowing, alkaline waters of moderate salinity and low to moderate organic pollution. These are all typical characteristics observed in the Sabie River (Barnard et al. 2019). The group Bacillariophyceae or diatoms forms the base of the food chain in most aquatic ecosystems, and they have the ability to respond quickly to changing environmental conditions. The higher flows also cause unfavourable conditions for cyanobacterial growth, which prefer relatively stagnant waters and are thus not prone to develop to bloom conditions in relatively fast-flowing streams as was the case at most of the sampling sites. During the low flow conditions of 2016 Cyanophyceae dominance and high cell concentrations were associated with Site 4 located in the land-use type agriculture and closely associated with higher concentrations of total phosphates. A change in dominance from Cyanophyceae to Bacillariophyceae at Site 4 was observed in 2017. Cyanophyceae were then second-most dominant class at sites 6, 7 and 8 in 2017. The reason for this shift in dominance of this class at Site 6 is not clear from the results. These sites are, however, downstream from areas more impacted on by agriculture and peri-urban settlements and nutrients and organic waste could have been transported to collect in the lower reaches of the river.

Bussi et al. (2016) found in their study that the class Cyanophyceae was the most sensitive to climatic variations and these variations can impact directly on to the physiological characteristics of phytoplankton (Winder & Sommer 2012). Shifts like this can have far-reaching effects on the ecosystem (Winder & Sommer 2012) as well as on the land-use activities associated with these sites, namely conservation. It was reported that wildlife mortality due to cyanobacterial blooms is increasing in the KNP (Bengis et al. 2016). The Chrysophyceae and Dinophyceae were associated with land-use types that included urban settlements during 2016. According to Katsiapi et al. (2012), Chrysophyceae is closely associated with forested areas. This was only the case in our study during the immediate post-drought conditions of 2017. As was found by other studies (Wher et al. 2015; Katsiapi et al. 2012), the Euglenophyceae were more closely associated with urban areas during 2016, but this changed during 2017 when this class was closely associated with sites (7 and 8) in the conservation land-use class.

Some genera were observed exclusively during the low flow conditions while others were exclusively observed during high flow conditions. A number of studies have found that morphological, physiological, behavioural and life-history traits of phytoplankton taxa strongly correlate with the gradients of anthropogenic stressors noted in both the catchment and the hydrological section of a river (Lange et al. 2015; Machado et al. 2016; Gökçe 2016). Thus anthropogenic factors can possibly explain the appearance of these genera. Genera that exclusively occurred during 2016 included those that are mostly filamentous (*Geitlerinema*, *Spirulina*, *Microspora* and *Mougeotia*). Other taxa encountered were more common in mesotrophic to eutrophic water (*Pseudanabaena* and *Snowella)* and some typical of waters with elevated levels of pollutants (*Phacus* and *Closterium)* and their occurrence is thus indicative of the prevailing conditions in the Sabie River (Reynolds & Descy 1996; Wher et al. 2015). *Closterium* species are even capable of surviving extended periods of drying (Wher et al. 2015). Genera that exclusively occurred during 2017 represented taxa that were mostly single-celled and small (pico-plankton such as *Gloeocapsa* and *Synechocystis*), more common to oligotrophic and poor nutrient waters with lower pH (*Frustulia, Hantzschia* and *Pinnularia*) with higher resilience in greater disturbance and higher flow conditions (*Ulothrix, Urosolenia*) and higher pollutant levels (*Cosmarium, Strombomonas*) (Reynolds & Descy 1996; Taylor et al. 2007; Wher et al. 2015).

During the high flow conditions of 2017, increases in acidity and a decrease in M alkalinity were observed in the Sabie River (Barnard et al. 2019) together with a decrease in total phosphates and ammonia. This could explain the exclusive appearance of certain diatom genera during 2017. In their study Lange et al. (2015) also found that higher nutrient concentration in waters impacted on by agriculture hosted phytoplankton dominated by large, non-attached, filamentous taxa after several weeks of low-flow conditions. They found that smaller cell size, nitrogen-fixing taxa with higher dispersal abilities were able to recover faster after disturbance due to their higher growth rates and resilience (Lange et al. 2015). Although filamentous, *Cylindrospermopsis* can fix nitrogen and was only found during 2017 when nutrients were lower.

Conclusion

With this study, we had a rare opportunity to study the influence of land-use on phytoplankton composition during a drought and the immediate post-drought period that followed. This study showed that changes in phytoplankton communities can reflect the land-use types in the catchment and that land-use impacts can be enhanced during higher flow conditions. Land-use and climate affected the nutrient concentrations in the river water and phytoplankton diversity responded rapidly to these changes. This environmental variability influenced the distribution of phytoplankton genera. Non-attached filamentous phytoplankton genera with limited dispersal abilities were mostly found during low flow rates with mesotrophic to eutrophic conditions, while small and nitrogen-fixing genera that can withstand high dispersal were observed mostly during high flow rate with oligotrophic conditions.

The results of this study are important if we want to predict the impacts of climate change on aquatic ecosystems. This study showed that an increase in phytoplankton concentration, especially that of the nuisance Cyanophyceae, is likely to occur during periods of low flows, and increased phosphate concentrations in agricultural and urban areas, but during high flow conditions, Cyanophyceae dominance can be displaced to downstream areas in lower river reaches. It is in the surrounding communities' interest to conserve the ecological functionality and the biological complexity of this freshwater ecosystem to safeguard water quality for domestic use and the health of domestic and wild animals, thus ensuring the economic well-being of the society depending on it.

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Authors' contributions

SB was the project leader, responsible for experimental and project design and main author. TM helped with the land-use analyses and was responsible for drawing all the maps and wrote parts of the manuscript. MS was responsible for land-use analyses. AV was responsible for phytoplankton data capturing and wrote parts of the manuscript.

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Supplementary material

Supplementary Table 1: List of all the genera found during the first year of sampling (2016) at the different sampling sites (1–8)

	Site	1	2	3	4	5	6	7	8
Cyanophyceae									
Anabaena	Ana	0	0	0	0	0	0	0	1
Aphanothece	Apha	0	1	1	1	0	0	1	1
Arthrospira	Art	0	0	1	1	0	0	1	0
Chroococcus	Chro	0	0	0	0	0	0	0	0
Geitlerinema	Gei	0	1	0	0	1	0	1	0
Johannesbaptista	Joh	0	1	0	0	0	0	0	0
Komvovoron	Komv	1	0	1	0	0	1	1	0
Leptolyngbya	Lep	0	0	0	0	0	1	0	0
Merismopedia	Mer	0	0	0	1	1	1	1	0
Oscillatoria	Osc	0	1	0	1	0	0	0	0
Phormidium	Pho	0	0	0	1	1	0	1	1
Pseudanabaena	Pse	0	0	0	0	0	0	1	1
Snowella	Sno	0	0	0	0	0	0	0	1
Spirulina	Spi	0	0	0	1	0	0	0	0
Total genera		1	4	3	6	3	3	7	5
Chlorophyceae									
Actinastrum	Act	0	0	0	0	0	0	1	0
Acutodesmus	Acu	0	0	0	1	0	1	1	1
Ankistrodesmus	Ank	0	0	0	0	0	0	0	0
Chlamydomonas	Chlam	0	0	0	0	1	1	1	0
Chlorella	Chlor	0	0	0	0	0	0	1	0
Chlorococcum	Chloro	0	0	0	1	0	0	0	0
Closterium	Clos	0	0	1	0	0	0	0	0
Coelastrum	Coe	0	0	0	0	0	0	0	0
Crucigenia	Cru	0	0	0	0	0	0	0	0
Crucigeniella	Cruc	0	0	0	1	0	0	0	0
Desmodesmus	Des	0	0	0	1	1	1	1	0
Elakatothrix	Ela	0	0	0	0	0	0	0	0
Eudorina	Eud	0	0	0	0	0	0	1	0
Microspora	Micr	0	1	0	0	1	0	0	0
Monoraphidium	Mon	1	1	1	0	0	0	0	0
Mougeotia	Mou	0	0	0	0	0	0	0	0

Supplementary Table 1: List of all the genera found during the first year of sampling (2016) at the different sampling sites (1–8) (continued)

	Site	1	2	3	4	5	6	7	8
Chlorophyceae (continued)									
Nephrocytium	Nep	0	0	0	0	0	0	0	0
Oedogonium	Oed	0	0	1	1	0	0	0	1
Oocystis	Ooc	0	0	0	0	0	0	0	0
Pandorina	Pan	0	0	0	0	0	0	1	0
Pediastrum	Ped	0	0	0	0	0	0	1	0
Scenedesmus	Sce	0	0	0	1	1	1	1	1
Schroederia	Schr	1	1	1	0	0	0	1	0
Spirogyra	Spiro	0	0	0	0	0	0	1	0
Staurastrum	Stau	0	0	0	0	0	0	0	0
Stigeoclonium	Stig	0	0	0	0	1	0	0	0
Tetraedron	Tet	0	0	0	0	0	0	0	0
Tetrastrum	Tetr	0	0	0	0	0	0	0	0
Treubaria	Treu	0	1	1	0	0	0	0	0
Total genera		2	4	5	6	5	4	11	3
Bacillariophyceae									
Achnanthes	Ach	1	1	1	1	1	1	1	1
Achnanthidium	Achn	1	1	1	1	1	1	1	1
Caloneis	Cal	0	0	0	0	0	0	1	0
Capartogramma	Cap	0	0	0	0	0	1	0	0
Cocconeis	Coc	1	1	1	1	1	1	1	1
Craticula	Cra	0	0	0	0	0	0	0	0
Cyclotella	Cyc	0	0	1	0	1	0	1	1
Cymatopleura	Cym	0	1	0	1	0	0	0	0
Cymbella	Cymb	1	1	1	1	1	1	1	1
Diatoma	Diat	0	1	1	0	0	0	0	0
Diploneis	Dip	0	0	1	0	0	0	1	1
Encyonopsis	Enc	0	1	1	1	0	1	1	0
Eunotia	Eun	1	0	0	0	0	0	0	0
Fragilaria	Fra	0	1	1	1	1	1	1	0
Geissleria	Gei	0	0	0	0	0	1	1	1
Gomphonema	Gom	0	1	1	1	1	1	1	1
Gyrosigma	Gyr	0	1	1	1	1	1	1	1
Hippodonta	Hipp	0	1	1	0	0	0	0	0
Melosira	Mel	0	1	1	1	1	0	0	1

Supplementary Table 1: List of all the genera found during the first year of sampling (2016) at the different sampling sites (1–8) (continued)

	Site	1	2	3	4	5	6	7	8
Bacillariophyceae (contined)									
Navicula	Nav	0	1	1	1	1	1	1	1
Nitzschia	Nit	0	1	1	1	1	1	1	1
Plagiotropis	Plag	0	0	0	0	0	0	0	0
Rhoicosphenia	Rho	0	1	1	0	0	0	0	0
Rhopalodia	Rhop	0	0	0	0	0	0	0	0
Sellophora	Sel	0	1	1	0	1	1	1	1
Surirella	Sur	0	0	0	1	0	1	1	1
Synedra	Syn	0	1	1	1	1	1	1	0
Total genera		5	17	18	14	13	15	17	14
Chrysophyceae									
Dinobryon	Din	0	0	0	0	0	0	0	0
Total genera		0	0	0	0	0	0	0	0
Dinophyceae									
Peridinopsis	Per	0	0	0	0	0	0	0	0
Peridinium	Peri	0	0	0	0	0	0	0	0
Total genera		0	0	0	0	0	0	0	0
Euglenaphyceae									
Euglena	Eug	0	0	0	0	0	0	0	1
Phacus	Phac	0	0	0	0	0	0	0	0
Tracelomonas	Trac	0	0	0	0	0	1	1	0
Total genera		0	0	0	0	0	1	1	1
Total genera for site		8	25	26	26	21	23	36	23

Supplementary Table 2. List of all the genera found during the second year of sampling (2017) at the different sampling sites (1–8)

	Site	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Cyanophyceae									
Anabaena	Ana	0	0	0	0	0	0	0	0
Aphanocapsa	Aph	0	0	0	0	1	1	1	1
Aphanothece	Apha	0	0	0	0	0	0	0	1
Arthrospira	Art	0	0	0	0	1	0	0	1
Chroococcus	Chro	0	0	0	0	0	1	0	0
Cylindrospermopsis	Cyl	0	0	0	1	0	1	0	0
Gloeocapsa	Glo	0	0	0	0	0	0	0	0
Johannesbaptista	Joh	0	1	0	0	0	0	0	0
Komvovoron	Komv	0	0	1	0	1	1	1	1
Leptolyngbya	Lep	0	0	0	1	0	0	0	0
Merismopedia	Mer	1	0	0	1	0	0	1	1
Oscillatoria	Osc	0	0	0	1	0	0	0	0
Phormidium	Pho	0	0	0	0	0	1	1	1
Radiocystis	Rad	0	0	0	0	0	0	0	0
Synechocystis	Synec	0	0	0	0	0	1	0	0
Total genera		**1**	**1**	**1**	**4**	**3**	**6**	**4**	**6**

Chlorophyceae									
Actinastrum	Act	0	0	0	0	1	0	0	0
Acutodesmus	Acu	0	0	0	1	0	0	1	0
Ankistrodesmus	Ank	0	0	0	0	0	0	0	0
Chlamydomonas	Chlam	0	0	0	1	1	1	1	1
Chlorella	Chlor	0	0	0	1	1	0	1	1
Chlorococcum	Chloro	0	0	0	0	0	0	0	0
Coelastrum	Coe	0	0	0	0	0	0	0	0
Cosmarium	Cos	0	0	0	0	0	0	0	0
Crucigenia	Cru	0	0	0	0	0	1	0	0
Crucigeniella	Cruc	0	0	0	1	1	1	0	0
Desmodesmus	Des	0	0	0	1	0	1	1	1
Dictosphaerium	Dict	0	0	1	1	0	1	1	0
Elakatothrix	Ela	0	0	0	0	0	0	0	0
Eudorina	Eud	0	0	0	0	0	0	1	0
Kirchneriella	Kir	0	0	0	0	0	0	0	0
Monoraphidium	Mon	0	1	1	1	0	1	1	0
Nephrocytium	Neph	0	0	0	0	0	0	0	0

Supplementary Table 2. List of all the genera found during the second year of sampling (2017) at the different sampling sites (1–8) (continued)

	Site	1	2	3	4	5	6	7	8
Chlorophyceae (continued)									
Oedogonium	Oed	0	1	0	1	0	0	1	0
Oocystis	Ooc	0	1	1	0	1	0	0	0
Pandorina	Pan	1	0	0	1	1	1	1	1
Pediastrum	Ped	0	0	0	1	0	0	1	0
Scenedesmus	Sce	0	0	1	1	1	1	1	1
Schroederia	Schr	1	1	1	1	0	0	0	0
Spirogyra	Spiro	0	0	0	0	0	0	0	0
Staurastrum	Stau	0	0	0	0	0	0	0	0
Stigeoclonium	Stig	1	0	0	0	0	0	0	0
Tetrastrum	Tetr	0	0	0	0	0	1	1	0
Treubaria	Treu	0	1	1	1	0	0	0	0
Ulothrix	Ulo	0	0	1	0	0	0	0	0
Total genera		**4**	**5**	**7**	**13**	**7**	**9**	**12**	**5**
Bacillariophyceae									
Achnanthes	Ach	1	1	1	1	1	1	1	1
Achnanthidium	Achn	1	1	1	1	1	1	1	1
Caloneis	Cal	0	0	0	0	0	0	0	0
Capartogramma	Cap	0	0	1	0	0	0	0	1
Cocconeis	Coc	1	1	1	1	1	1	1	1
Cyclotella	Cyc	0	0	0	1	1	1	1	0
Cymatopleura	Cym	0	0	0	1	0	0	0	0
Cymbella	Cymb	0	1	1	1	1	1	1	1
Diatoma	Diat	0	0	0	0	0	0	1	0
Diploneis	Dip	0	0	0	0	0	0	1	0
Encyonopsis	Enc	0	1	1	1	1	1	1	1
Eunotia	Eun	1	0	0	0	0	0	0	0
Fragilaria	Fra	0	1	1	1	1	1	1	0
Frustulia	Fru	1	0	0	0	0	0	0	0
Geissleria	Gei	0	0	0	0	0	0	0	0
Gomphonema	Gom	1	1	1	1	1	1	1	1
Gyrosigma	Gyr	0	0	1	1	1	1	1	1
Hantzschia	Han	0	0	0	0	0	0	1	0
Melosira	Mel	1	1	1	1	1	1	1	0
Navicula	Nav	1	1	1	1	1	1	1	1

Supplementary Table 2. List of all the genera found during the second year of sampling (2017) at the different sampling sites (1–8) (continued)

	Site	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Bacillariophyceae (continued)									
Nitzschia	Nit	0	1	1	1	1	1	1	1
Pinnularia	Pin	0	0	1	0	1	0	1	0
Plagiotropis	Plag	0	0	0	0	0	0	1	1
Planothidium	Plan	1	0	0	0	0	0	0	0
Rhoicosphenia	Rho	0	1	1	0	0	0	0	0
Sellophora	Sel	0	0	0	0	1	1	0	0
Surirella	Sur	0	0	0	0	1	1	1	1
Synedra	Syn	0	1	1	1	1	1	1	1
Urosolenia	Uro	0	0	0	0	0	0	0	0
Total genera		**9**	**12**	**15**	**14**	**16**	**15**	**19**	**13**
Chrysophyceae									
Dinobryon	Din	0	0	0	0	0	0	0	0
Total genera		**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Dinophyceae									
Peridinopsis	Per	0	0	0	0	0	0	0	0
Peridinium	Peri	0	0	0	0	0	0	0	0
Total genera		**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Euglenophyceae									
Euglena	Eug	0	0	0	0	0	0	0	0
Strombomonas	Stro	0	0	0	0	0	0	0	0
Tracelomonas	Trac	0	0	0	1	0	1	0	1
Total genera		**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**
Total genera for site		**14**	**18**	**23**	**32**	**26**	**31**	**35**	**25**

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Restoration after bush control in selected rangeland areas of semi-arid savannas in South Africa

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Background: One of the main causes of land degradation in South Africa is bush thickening (BT) of mainly *Senegalia* or *Vachellia* species. Restoration methods are required to control BT, and to improve grass biomass production and soil conditions in South Africa.

Objectives: The objectives of this study were to determine the effect of brush packing (BP) as a restoration method to increase grass biomass production, assess soil moisture after BP on different soil types, and document the perceptions of the local communities towards BP.

Method: Methods included cutting the stems of woodies with a diameter of at least 10 cm at knee height by chainsaw and manual clipping after which an arborocide was applied to the stumps. A neutron probe was used to measure volumetric moisture content at two different soil depths. The grass biomass was analysed using ANOVA at a confidence level of 95%. Quantitative and qualitative approaches were used to gather information about the perceptions of local communities towards restoration in group discussions.

Results: The short-term data showed that the implementation of BP as restoration method increased grass biomass production. The soil texture influenced the volumetric soil moisture. Higher soil moisture content was found in the deeper clayey soils. The local participants' interpretation towards the restoration project was positive.

Conclusion: The project increased the grazing potential and contributed to job creation to improve the well-being of the people in the community.

Key words: biomass production, degraded lands, bush thickening, brush packing, land users' perceptions.

Introduction

The degradation of rangelands in the arid and semi-arid areas of the world, and especially in southern Africa, is increasing at alarming rates, mainly due to land mismanagement, untenable land-tenure systems and climate change (Hoffman & Ashwell 2001). Human-induced degradation by management and land tenure types often leads to changes in the species composition (Siebert et al. 2021). Land degradation threatens livestock and game production that depends on the natural ecosystem for forage production while it also has a negative impact on ecosystem services (ES) such as the provision of potable water and food (Havstad et al. 2007; Schwilch, Hessel & Verzandvoort 2012). These basic ecosystem services are important and can be maintained by implementing sustainable land-management (SLM) practices (Liniger & Studer, 2019). At the Rio Earth Summit in 1992, SLM was defined as 'the viable use of resources, including soils, water, animals and plants for the production of goods and services to meet changing human needs, while simultaneously ensuring the long-term productive potential of these resources and the maintenance of environmental functions'.

The rain-fed arid- and semi-arid regions in southern Africa are characterised by variable, often unpredictable, rainfall events (in-space, inter-annually and intra-seasonally), leading to unexpected droughts (Kellner et al. 2018). The resultant degradation of water resources and the deterioration of the condition of soil and vegetation have a negative impact on the sustainability of land and ecosystem services. However, well applied SLM practices can conserve and protect the multiple services and functions provided by the land (Von Maltitz, Lindeque & Kellner, 2018).

Land degradation is often associated with overgrazing and the concomitant negative impacts on ES (Swift, Izac & Van Noordwijk 2004). Nevertheless, Shackleton et al. (2008) caution that understanding the complexity between climate change and management applications that leads to land degradation requires careful investigation.

Different land-tenure regimes are found in southern Africa, that have different impacts and extents on land degradation, including the increase in the density of woody species (also called woody or bush thickening – BT), which affects the ES (Von Maltitz, Lindeque & Kellner, 2018; Von Maltitz et al., 2019). Broadly, these tenure systems resort under one of three main categories: (1) private and leasehold land, also referred to as 'commercially managed areas'; (2) communal land, which is mainly traditional-owned land managed by local authorities, including some form of commercial management; and (3) conservation areas (private and state-owned).

An assessment of land degradation in drylands found that communal-managed areas are highly degraded with a loss in productivity and biodiversity, associated with increased soil erosion (Liniger & Studer 2019; Petri, Biancalani & Lindeque 2019). An underlying cause of this degradation in the sustainability of drylands is bush thickening.

Bush thickening

Using aerial photographs dated from 1940 to 2010, Buitenwerf et al. (2012) found that woody cover had doubled in commercial, communal and conservation rangeland areas. Skowno et al. (2017) found that only 2.7 million ha had been affected by BT between 1990 and 2013, but recent findings by Turpie et al. (2018) suggest that BT ranges from 5.7 to 13 million ha in South Africa.

Savanna, South Africa's most prominent biome, is used extensively as rangeland for the production and conservation of livestock and/or wildlife, as well as subsistence crop farming (Kgosikoma, Harvie & Mojeremane 2012; Liniger & Studer 2019). The vegetation structure and composition of these savannas vary considerably due to variances in topography, soil and climate (Mucina & Rutherford 2006). Large parts of the savannas in the more arid- and semi-arid regions towards the west and north of the country are degraded due to the densification of alien and indigenous woody shrub and tree species, resulting in so-called 'bush thickening' (BT) (Joubert, Rothauge & Smit 2008). In these areas, the Savanna Biome is dominated by *Senegalia mellifera* (Vahl) Seigel & Ebinger and/or *Vachellia* species, including other woody and some herbaceous species.

Bush encroachment, however, refers to instances where woody species (shrubs and trees) establish in areas where they did not previously occur (De Klerk 2004; Smit, Richter & Aucamp 1999). Bush thickening (BT) is caused by a dynamic change in vegetation composition, structure and density over time (De Klerk 2004; Smit, Richter & Aucamp 1999). Bush thickening is caused by established stands of woody species, which increase in density and cover mostly as a result of fire and grazing management, below-average rainfall, competition between C_3 and C_4 type plants and elevated CO_2 levels (Buitenwerf et al. 2012; Dreber, Van Rooyen & Kellner 2018; Higgins, Bond & Trollope 2007; Kellner 2008; Kraaij & Ward 2006; Ward 2005).

Due to the imbalance in the grass–woody ratio and the loss of grass cover, especially palatable forage species, BT causes a decline in the functionality of savanna rangelands (Britz & Ward 2007; Eldridge et al. 2011; Harmse, Kellner & Dreber 2016). Furthermore, the decrease in grass densities reduces the soil's infiltration rate and increases raindrop impact, ultimately increasing surface runoff and soil erosion (Donahue & Auburn 2003). According to Gregory et al. (2015), each soil type will respond differently to a lack of cover due to its properties. Clayey soils are more prone to compaction due to cohesion, while a sandy soil is more prone to structure loss leading to erosion by wind or water. Bush thickening also has significant socio-ecological implications for land users since the resultant degradation decreases the value of the land for grazing and livestock keeping, as well as for game viewing and eco-tourism (De Klerk 2004; Arbieu et al. 2017).

To control BT and compensate for economic losses, land users apply active or passive restoration methods (Wigley, Bond & Hoffman 2009). Although sound rangeland management practices can reduce BT, local capacity and knowledge to enforce control/clearing measures are often lacking. The type of bush-clearing technology employed, whether chemical, manual, mechanical or a combination thereof, must be determined by the density and type of woody species causing the thickening or encroachment (Barac, Kellner & De Klerk 2004; De Klerk 2004). Clearing thickened bush normally increases biomass production of grasses, depending on the soil type and rainfall pattern, as well as the technology implemented. Bush clearing and the eradication of alien species can lead to economically feasible enterprises such as the production of charcoal, animal feed, timber for construction purposes and wood for cooking and heating. Establishing enterprises such as these could also result in job creation (Sudha et al. 2003; De Klerk 2004; Rothauge & Gschewender 2014).

Restoration

The Society for Ecological Restoration (2004) defines ecological restoration as the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed. Re-seeding methods of palatable, perennial grasses is often applied in restoration at a small scale, especially when the soil seed bank is depleted (Kellner 2008).

In South Africa, the Natural Resource Management Unit, resorting under the Department of Environment, Forestry and Fisheries (DEFF), is responsible for the restoration of degraded lands, with the inclusion of related research and development projects (Van Wilgen et al. 2001). In addition, the Land Care Programme resorting under the Department of Agriculture, Land Reform and Rural Development is also involved in controlling bush thickening (BT) and implementing SLM practices (Mulder & Brent 2006). One of the approaches for the restoration of rangelands after bush clearing, that is supported by these departments, is brush packing (BP).

BP entails covering the soil surface with organic material such as woody branches and leaves of plants to promote grass growth and biomass production (Visser et al. 2007; Kellner 2008). BP also protects seedlings from disturbances (defoliation and trampling) and modify microclimate to make conditions (such as moisture content, soil structure and temperature and nutrient content) suitable for germination and establishment (Tongway & Ludwig 2011; Modungwa 2017). If branches and roots from plants with nitrogen fixing abilities (e.g. *Vachellia* and *Senegalia* species) are used, the decomposing brush will not only enrich the nutrient component of the soil and increase the functionality of the vegetation that established under the woody twigs, but will also help to control erosion (Modungwa 2017).

Although labour intensive, BP is a cost-effective restoration method since no fenced paddocks nor rotational grazing is required to protect/rest the land. Due to its labour-intensive nature, clearing invasive woody species also provides job opportunities for local people, thereby contributing to the well-being of the affected communities.

This study sets out to compare different restoration methods involving BP after bush clearing. The specific objectives of the study were to determine (i) the effect of BP and re-seeding on the grass biomass production following bush control; (ii) measure changes in moisture flux with soil depth after the application of BP at selected study areas representing different soil types; and (iii) assess farmers' perceptions of BP as a restoration method following bush control.

Research method, design and study site

Application of BP as a restoration method

A number of BT areas were identified by the DEFF in the Lephalale Municipality (including Shongoane village and the D'Nyala Nature Reserve (NR)) in the Limpopo Province and the Taung Municipality (which includes the Manthe village) in the North West province of South Africa. Shongoane and Manthe villages are communally managed lands affected by BT, and D'Nyala NR was a priority area for conservation and for controlling woody species (Figure 1). The Nature Reserve was selected as control, as protected, untransformed areas are known to be a good benchmark for biodiversity (Siebert et al. 2021).

The study sites at the Shongoane and Manthe villages were selected as suitable regions to also undertake the socio-economic surveys because the woody species causing BT (e.g. various *Senegalia* spp. and *Vachellia* spp., as well as *Diospyros lycioides* Desf. subsp. *guerkei* (Kuntze) De Winter and *Dichrostachys cinerea* (L.) Wight & Arn. are highly abundant, and land users often have to abandon their land due BT and subsequent decrease in grazing capacity. The most prominent encroacher species on the communal lands in both Limpopo and North West province included thorn trees such as the umbrella thorn (*Vachellia tortilis* (Forssk.) Gallaso & Banfi), black thorn (*Senegalia mellifera* (Vahl) Seigel & Ebinger subsp. *Detinens* (Burch.) Kyal. & Boatwr.) and sweet thorn (*Vachellia karroo* (Hayne) Banfi & Glasso). The density and cover of these species could unfortunately not be determined before the trial. The camphor bush (*Tarchonanthus camphoratus* L.) also occurred in both areas and contributed to BT. All the study sites are classified as semi-arid, with rainfall averaging less than 430 mm/annum and temperatures ranging between 31 and 35°C during the warmest months (Engelbrecht & Engelbrecht 2016). The majority of people in the communally managed communities are unemployed, with subsistence livestock husbandry and small-scale cropping being the dominant land uses. Around 400 people from local villages near Lephalale and at D'Nyala NR and 100 people from the Manthe village were employed to partake in bush clearing.

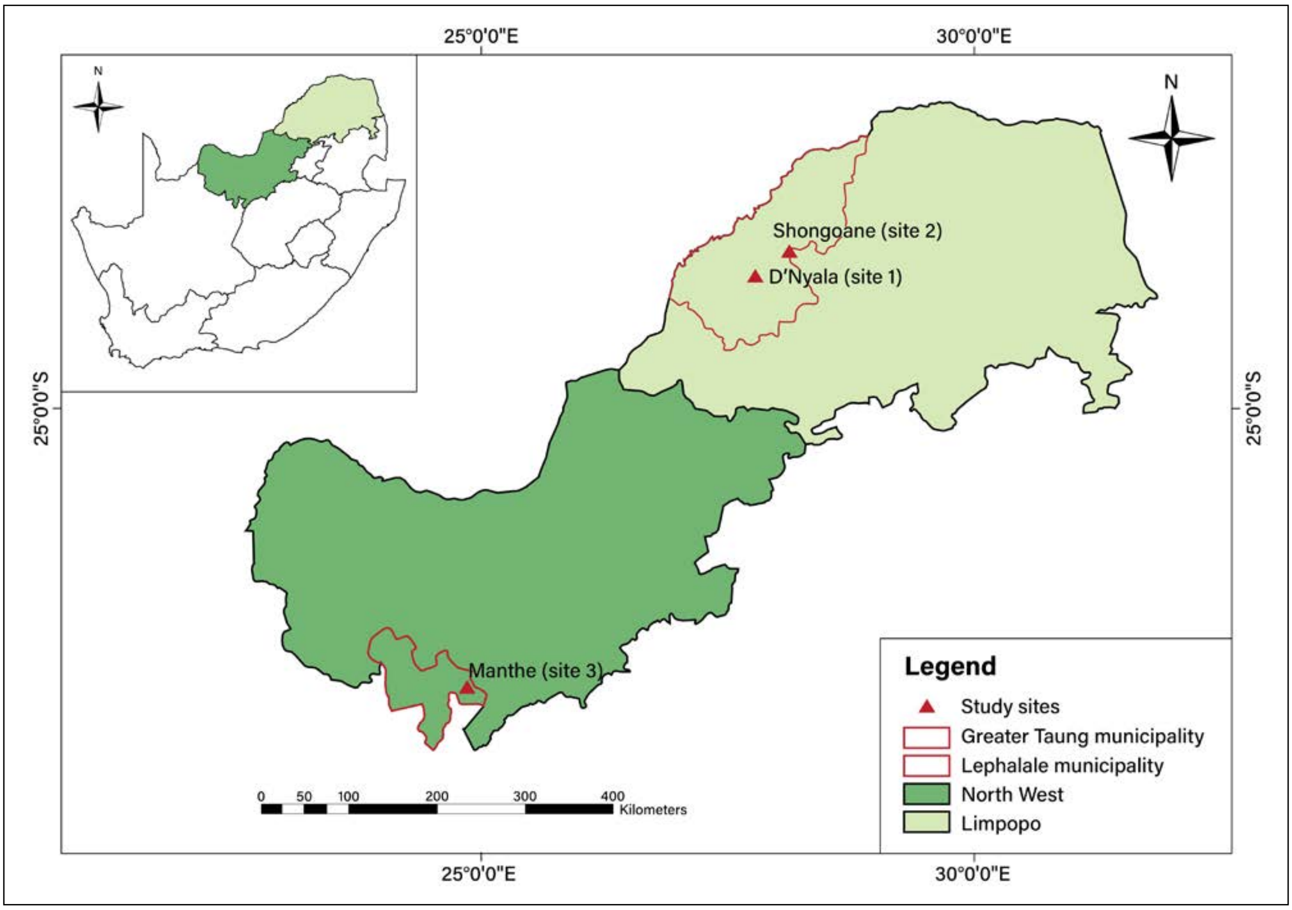


Figure 1. Location of the study sites in the Limpopo and North West provinces of South Africa. Manthe (Site 3) is in the North West, and D'Nyala NR (Site 1) and Shongoane (Site 2) in the Limpopo.

Experimental layout and design

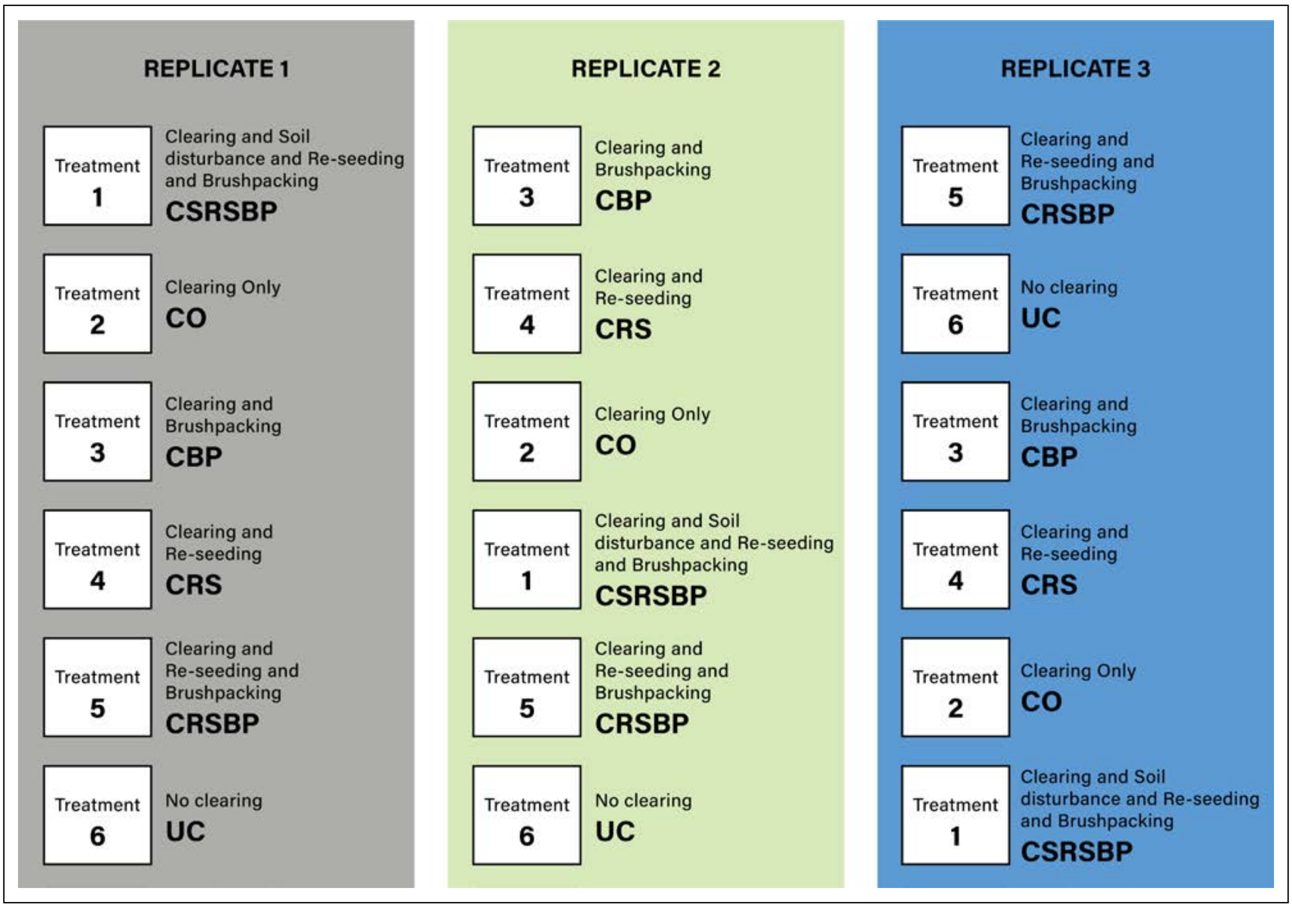
The three study sites (D'Nyala NR, Shongoane and Manthe) had the same experimental designs. Six restoration experimental plots were constructed between September and November 2017 at each site (Figure 2). Each of the restoration plots were 400 m^2 (20 m × 20 m) in size and arranged in a completely randomised block experimental design. Six different restoration methods were tested, replicated three times at each site. The treatments included different combinations of: (i) clearing, soil disturbance, brush packing and re-seeding (CSRSBP); (ii) clearing only–control (CO); (iii) clearing and brush packing (CBP); (iv) clearing and re-seeding (CRS); (v) clearing, brush packing and re-seeding (CRSBP); and (vi) no clearing/uncleared control (UC). At each of the three sites a total of 18 experimental plots were created (54 total) and half involved the BP method, which equalled almost half a hectare.

Woodies (shrubs and trees) of 3 m and less with a diameter of 10 cm at knee height were cleared using handsaws, clippers and a chain saw. After clearing/control, an arborocide (Kaput gel) that has the least impact on the environment was applied on the cut-stumps. Woodies taller than 3 m were considered as contributors for biodiversity, especially for the nesting of birds. In Treatment 1 (Figure 2), the soil was lightly loosened with a rake (minimal soil disturbance) before re-seeding. A mixture of five annual and perennial grass species were used for the re-seeding of treatments 1, 4 and 5, i.e. *Cenchrus ciliaris* L., *Chloris gayana* Kunth, *Cynodon dactylon* (L.) Pers., *Digitaria eriantha* Steud, and *Eragrostis curvula* (Schrad.) Nees. The seed of the grass species were mixed and broadcasted in the experimental plots (200g/400 m^2). The grass species selected are native to and dominant in South African savannas. These grass species are a standard veld mixture used in conservation management (Van Oudtshoorn, 2012). For the BP restoration methods, branches of the cleared woody species at the sites were used. The same restoration and re-seeding methods were used at all the study sites (Figure 1).

Measured variables

Biomass production

After the trial was initiated in 2017, grass biomass was collected at the end of the 2018 and 2019 seasons. All grass was cut at a height of 5 cm above the ground in five randomly distributed 1 m^2 quadrats per treatment and put in separate bags. During the growth season, no



REPLICATE 1	REPLICATE 2	REPLICATE 3
Treatment 1 Clearing and Soil disturbance and Re-seeding and Brushpacking CSRSBP	Treatment 3 Clearing and Brushpacking CBP	Treatment 5 Clearing and Re-seeding and Brushpacking CRSBP
Treatment 2 Clearing Only CO	Treatment 4 Clearing and Re-seeding CRS	Treatment 6 No clearing UC
Treatment 3 Clearing and Brushpacking CBP	Treatment 2 Clearing Only CO	Treatment 3 Clearing and Brushpacking CBP
Treatment 4 Clearing and Re-seeding CRS	Treatment 1 Clearing and Soil disturbance and Re-seeding and Brushpacking CSRSBP	Treatment 4 Clearing and Re-seeding CRS
Treatment 5 Clearing and Re-seeding and Brushpacking CRSBP	Treatment 5 Clearing and Re-seeding and Brushpacking CRSBP	Treatment 2 Clearing Only CO
Treatment 6 No clearing UC	Treatment 6 No clearing UC	Treatment 1 Clearing and Soil disturbance and Re-seeding and Brushpacking CSRSBP

Figure 2. Experimental design and plot layout of the six restoration methods (treatments) in the three replicates in three blocks at each study site.

fertiliser was added to the soil and no irrigation applied. The grass samples in bags were oven dried at 67°C until constant weight and weighed to determine dry matter production.

Grass species abundance/density

Grass density was determined in the 2018 and 2019 seasons at each site in five 1 m^2 quadrants of each experimental plot representing different restoration methods. Measurements were taken within the quadrant by counting the number of individual annual and perennial grass species appearing in the 1 m^2 area. The total was added at the end of the five measured counts. Other herbaceous species were not included in these counts as this was not part of the research objective.

Soil surveys

Soil moisture is an important variable which affects infiltration, runoff, soil temperature and the amount of water available to plants. According to Gao et al. (2017), these variables are affected by BT due to the increase of high-density woody plant roots. Since soil moisture has a strong spatial-temporal variability and is affected by the soil type, moisture readings commenced at the end of 2019 rainy season (Gao et al. 2017). A neutron probe was used to measure soil water content at different depths at the three study sites (Manthe, Shongoane and D'Nyala NR) (Chanasyk & Naeth 1996; Reichardt 2007). The soil moisture measurements were taken in the centre of one plot per treatment per site and totalling 18 (see Figure 2 above for the experimental design and layout).

The method of measuring soil moisture by means of the neutron probe entails that a hole is drilled into the soil using an auger followed by the installation of a tube (Reichardt 2007). The neutron probe was lowered into the soil in an access tube and readings were taken at different depths (Chanasyk & Naeth 1996; Reichardt 2007). In this study, readings were taken at 10 cm intervals. A calibration equation was used to convert the thermal neutron count rate to soil moisture (Reichardt 2007). The equation used in this study was:

$$y = 0.3002x - 0.2158$$

Where y is the volumetric moisture content and x is the thermal neutron count ratio.

Volumetric or concentration water content (v/v) is a measurement of soil moisture and is the ratio of water volume to soil volume and is represented by the following equation:

$$\Theta_v = \Theta_m / D_b * 100$$

Where Θ_v is the volumetric water content percentage, Θ_m is the volume of soil moisture and D_b is the total soil.

For example, if volumetric soil moisture content is 13.1 v/v, then a volume of 13.1% of the total soil is soil moisture. Soil moisture contained in the soil pores or soil aggregates of the upper 10 cm of soil is called surface soil moisture. The upper 200 cm of soil moisture is named the root zone as most roots are found here although specialised species may penetrate deeper.

Soil texture and clay percentage were determined in the field by means of the 'hand texturing' method (Brown 2019). The method entails using a handful of moist soil followed by manipulating the soil into various shapes and judging the soil texture by the ability or coherence of the soil to remain in a certain shape (bolus, cylindrical and bent cylindrical shapes) (Brown 2019). Soil forms were determined using a 'Munsell Color Chart' (Munsell Color 1994) and *Soil classification: a taxonomic system for South Africa* (Soil Classification Working Group, 1991).

Social and livelihoods survey (perceptions of land users)

The perceptions on the socio-economic impact and land users' practices of the communal land users were assessed. The recruitment and participation process commenced in 2018. The first stage to initiate interest and participation was through the *nduna*/chief of the community. Thereafter, follow-ups were carried out through a mediator. Two different methods to gather data were used at the study sites. The quantitative, non-experimental, cross-sectional design was used at the Manthe study site (Mann 2003). A hundred randomly selected individuals (livestock owners and small-scale farmers) were interviewed at households in the village using semi-structured questionnaires where the BP project has benefited the community. Interviews were conducted in participants' own local language (Setswana). Questionnaires were used to provide quantitative data on the perceptions and socio-economic value of the environment.

At the Shongoane study site, a qualitative approach was used (Johnson & Waterfield 2004). According to Moon et al. (2016) and Petty, Thompson and Stew (2012), qualitative research is defined by the nature of the questions asked in the research. The concept and methodologies were thus adopted during the design of the research, and the analysis and interpretation were associated with assumptions made when collecting the data (Khagram et al. 2010). Data was gathered through semi-structured interviews containing five questions. However, depending on the response given by the participant, a follow-up question was asked to gain a better understanding. The questions focused on the participant's general perception of the environment and the contribution made by the bush-clearing project since its inception. Data saturation was reached when no new information was discovered. Participants that were part of the sample consisted of a mixed group of males and females, ranging in age from 22 to 55. The interviews conducted with the participants were recorded.

Statistical analysis

The effect of the different treatments on biomass production was tested using a two-way analysis of variance (ANOVA). ANOVA was conducted using Genstat (Payne 2014). Multiple comparisons of means were performed using least significant difference (LSD) and Tukey's HSD range test. Tukey's test showed that only plots with BP treatment had an influence on grass biomass production ($p<0.05$). Data from the two seasons were analysed separately because of significant ($p<0.05$) season-year interactions.

The social study was analysed differently from the biophysical data. For the Shongoane survey the data were thematically analysed. A thematic analysis is a method commonly used in the analysis of qualitative data (Vaismoradi et al., 2013, Gibbs, 2007). The audio recordings obtained from the interviews at Shongoane were transcribed and analysed using thematic content analysis procedure, which included data coding, categorisation and thematic description and the identification of themes and sub-themes (Braun & Clarke 2006; Gibbs 2007).

Basic statistically analysis and correlations for the quantitative social assessments were used for the surveys carried out at the Manthe study site (Field 2005).

Ethical consideration

As a primary requirement for social studies, the ethical clearance was awarded by the North-West University's Research Ethics Regulatory Committee. The ethical clearance numbers were PSB002-037-01-2018 and NWU-00120-18-A1 for the Manthe and Lephalale study sites respectively. Regulations of the university's registered ethics committee regarding research with human participants were considered during all phases of the study.

Results and discussion

Above-ground grass biomass production

The difference in the mean above-ground grass biomass production (g.m^{-2}) during 2018 and 2019 at the three sites is illustrated in Figure 3. There was a significant difference ($p<0.05$) in grass biomass across the treatments at all sites. Two factors mainly influencing the grass biomass production were season and treatment (season-treatment interaction effect). From here on, the seasons will be considered separately to only consider the treatment effect.

The CO treatment at the Manthe site had the lowest grass production (7.5 g.m^{-2}) in the 2018 season. However, in the 2019 season, the lowest grass production (21.8 g.m^{-2}) was in the UC treatment at Manthe compared to the highest production of 296.4 g.m^{-2} in 2019 in the CSRSBP treatment. At Shongoane, the lowest grass biomass production (25.2 g.m^{-2}) was in 2018 for the UC treatment, and in 2019 the treatment CRS produced the lowest grass biomass of 44.1 g.m^{-2} (Figure 3). At the D'Nyala NR site, unlike the other sites where grazing animals were managed better, the lowest biomass was 28.2 g.m^{-2} in 2018 for the CRS treatment, with only a 3 g.m^{-2} improvement in the 2019 season for the same treatment.

The highest produced biomass was obtained during the second season of monitoring (2019) within the CSRSBP treatment for the Manthe and Shongoane sites, which are communally managed lands, and the highest biomass production for the D'Nyala NR site was produced for the CBP treatment in 2019. In the BP treatments the grass biomass production increased in the second season (Figure 3), with the highest increase at the Shongoane site (553.9 g.m^{-2}), and also by 296.4 g.m^{-2} and 272 g.m^{-2} at the D'Nyala NR and Manthe sites respectively.

Biomass production increased with a notable effect in all brush packing treatments (CSRSBP, CBP and CRSBP). Generally, the CSRSBP, CBP and CRSBP produced a statistically similar grass biomass ($p>0.05$), but all of them produced significantly higher biomass than the rest of the treatments ($p<0.05$). The CBP treatment compared to the other BP treatments (CSRSBP and CRSBP) produced the highest grass biomass. With the high grass biomass production, grazing capacity and fodder production is improved (Ward 2005). Notably, a combination of re-seeding and brush packing did not yield higher grass production at any sites than expected. This could be because perennial grasses take longer to establish, and a two-season study does not show the effects immediately. Another reason is that the sites are in semi-arid regions, and the seeds could have dried in the ground before receiving enough moisture to germinate.

Grass species abundance/ density in 2019

The overall percentage of grass individuals (annuals, perennials and species richness) for the different restoration treatments at the three sites could be distinguished for 2019 (Table 1). The mean percentage of annuals were much higher at the Manthe site, whereas more perennials occurred at the Shongoane site (mean of 144.5%) (Table 1). Annual species such as *Aristida bipartita* (Nees) Trin. & Rupr., *A. congesta* Roem. & Schult. subsp. *congesta* and *Tragus berteronianus* Schult. occur mostly in the UC and CO sites, and perennial species, such as *Cynodon dactylon* (L.) Pers., *Eragrostis trichophora* Coss. & Durieu, *E. curvula* (Schrad.) Nees and *Microchloa caffra* Nees. occurred in sites where BP was applied.

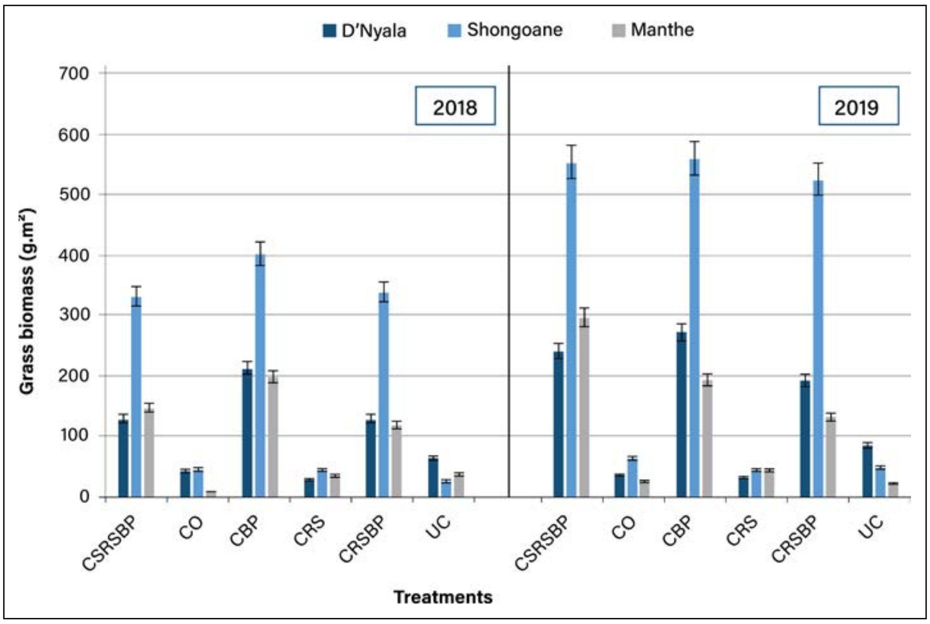


Figure 3: Above-ground grass biomass production (g.m^{-2}) for the 2018 and 2019 seasons at the research sites D'Nyala NR, Shongoane and Manthe in different restoration treatments following bush clearing. Error bars indicate the 95% confidence interval of each mean value.

Legend: Clearing and soil disturbance and brush packing and re-seeding **(CSRSBP)**, Clearing only **(CO)**, Clearing and brush packing **(CBP),** Clearing and re-seeding **(CRS)**, Clearing and brush packing and re-seeding **(CRSBP)** and No clearing/ non-clearing (control plot) **(UC)**

Table 1: Average grass abundance (%) per m^2 for annuals (A) and perennials (P), as well as total number of species per restoration treatment for 2019 at the Manthe, Shongoane and D'Nyala NR sites (see text for explanation of abbreviations for treatments)

Treatment	Manthe			Shongoane			D'Nyala NR		
	A	P	Species richness	A	P	Species richness	A	P	Species richness
UC	46	43	11	42	79	14	9	127	9
CO	98	8	8	47	83	15	40	34	8
CRS	61	81	12	91	113	17	12	55	11
CBP	74	43	10	21	183	16	34	87	14
CRSBP	105	89	12	40	160	18	18	110	11
CSRSBP	110	27	13	47	129	15	14	75	12

The results revealed that BP restoration method contributed to higher perennial grass species abundance, especially at the Shongoane study site, which is characterised by high clay soils (Table 1). This suggests that brush packing's ability to increase rangeland grazing potential is dependent on soil type.

Influence of BP restoration methods on soil moisture content in 2019

The overall soil forms of Manthe, D'Nyala and Shongoane were: Mispah, Avalon and Rensburg, respectively. Mispah soils at Manthe had an average clay percentage of 38% in the A-horizon and 45% in the B-horizon. Mispah soil forms have a low water-holding capacity due to their shallowness. The soils at the study site of the D'Nyala NR consisted of 15% (A-horizon) and 18% (B-horizon) clay content respectively. The Avalon soil form is well drained and moderately slow to moderately permeable soils due to its depth and soil texture. The Rensburg soil studied at Shongoane indicated an A-horizon of more than 50% clay content, a B-horizon of more than 45% and a C-horizon of average 38%. The Rensburg soil form of Shongoane exhibits deep swelling clays with high water holding capacity that increases with depth due to the swelling.

The volumetric soil moisture content was higher at deeper depths (20–30 cm) than in the shallower 0–10 cm surface soil for all study sites. The treatments that included BP illustrated higher moisture content differences with depth compared to non-brush packing treatments for D'Nyala NR, thus soils treated with BP contained more moisture (water) deeper into the soil profile than that of non-brush packing (Figure 4). Surface soil moisture (0–10 cm of soil below the surface) values were also higher in treatments with BP than those without BP.

At the Manthe study site the soil surface moisture (0–10 cm) content values illustrate no difference regarding the type of treatment. Manthe exhibited shallow (average 11 cm in depth) Mispah soils, containing rock fragments or gravel. During moisture measurements (February 2019) the maximum temperatures reached 32°C and no precipitation had occurred for a number of weeks, indicating that evapotranspiration had averaged the moisture content in the shallow soils. The UC (uncleared control) treatment indicated highest soil moisture content deeper into the soil profile (20–30 cm) compared to the treatments.

At the Shongoane study site, the soil moisture had a greater (more than 100v/v difference) moisture content difference between the surface soil (0–10 cm) compared to deeper soil (20–30 cm), most likely due to an increase in clay content (swelling or expansive clay) with depth, compared to soils of D'Nyala NR and Manthe (Figure 4). No clear relationship was evident between treatment and soil moisture increase with depth. Overall soil moisture content of Shongoane was therefore higher with depth than the soil moisture of D'Nyala NR and Manthe, not due to the applied treatments, but due to soil type.

At the other two study sites (D'Nyala NR, Manthe) with higher sand content, soil moisture increased, but was not maintained with depth due to the leaching of water further into the soil profile. Shongoane site is comprised of a finer sand grade and higher clay content, which explains the increase in volumetric soil moisture content values. The first 10– 20 cm (A-horizon) consists of more than 48% clay, while the deeper B-horizon consists of more than 55% clay content. This phenomenon substantiates the increase of soil moisture with depth. D'Nyala exhibited the lowest amount of clay content and consisted of a fine to medium sand grade, which explicates the lower volumetric soil moisture values compared to that of the other sites. Wang et al. (2019) conducted a study on the effects of climate and vegetation on soil moisture on an arid area and concluded that precipitation, soil temperature and vegetation had influences on soil moisture variability. Soil temperature is expected to play a significant role in surface moisture content but was not part of this study based on site-specific limitations.

The rate of evaporation of moisture content in the surface soil (0–10 cm) is controlled by atmospheric conditions when the soil is sufficiently close to saturation (Brutsaert 2013). When surface soil is no longer sufficiently saturated, the effect of atmospheric conditions decreases and evaporation is controlled by the rate of water movement to the soil surface through the soil profile (Brutsaert 2013). Soil texture and vegetation affects water movement through soil pores in soils (leaching and capillary flow). The overall observation concluded that soil texture illustrates a strong affiliation with volumetric soil moisture content. A finer sand texture and higher clay content yielded higher volumetric soil moisture content values.

Perceptions of local land users

Most work examining the impact of woody encroachment or thickening on ecosystem services has focused on the biophysical and economic implications without examining land users' perceptions (Eldridge et al. 2011; Anadon et al. 2014). Insight into the land user's perceptions adds valuable information that will contribute to the importance of its application for future restoration projects to elevate the needs of the people living in these ecological systems.

At the Manthe study site, the majority of participating land-users were males (61.9%) of whom only some had primary (28.9%) or no formal education (17.5%). Most participants (86.5%) had a monthly household income of less than R2 000/month, with 46.9% relying on government grants and pensions as their main source of income. Nearly 62% of the participants keep livestock (mainly cattle and sheep) for financial security while the rest keeps livestock for food production (milk/meat).

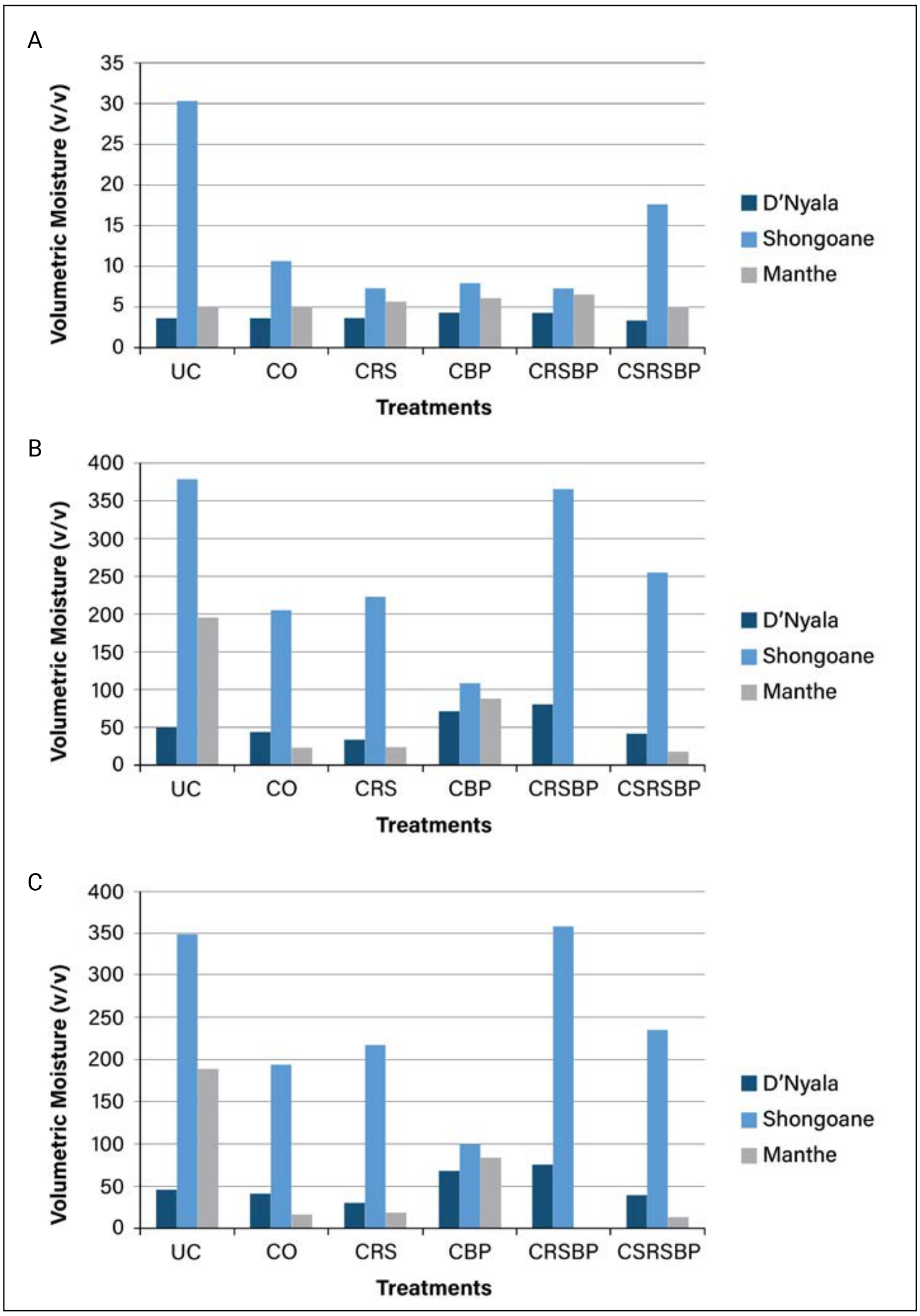


Figure 4. The volumetric soil moisture at two depths (a: 0–10 cm, b: 20–30 cm and c: the difference between the 10 cm and 20 cm depth in volumetric soil moisture) for the six restoration treatments at the three study sites for 2019 (Manthe, Shongoane and D'Nyala NR).

In Limpopo (i.e. Shongoane village and the D'Nyala NR), a qualitative approach was used to gather data. The interviews conducted at Shongoane village and D'Nyala NR revealed that 65% of those directly involved in the bush-clearing project were women. From the interviews the following sub-themes emerged regarding bush clearing: employment opportunities; experience and training; and improved environmental conditions. The participants were of the opinion that the restoration programme offered employment, which enabled them to sustain their livelihoods. Furthermore, the programme offered an opportunity for community members, especially the previously unemployed, to be trained and to gain experience. The qualitative data revealed that participants' attitude towards the environment and its improvement is positively influenced by a project of this kind.

The overall impression of the participants about the restoration project to control BT was that it is beneficial to the community and should be maintained over the long term. The project not only inspired and encouraged participants, but residents of the Manthe and Shongoane villages at large took an interest and accepted responsibility for the restoration of the degraded rangelands and to gain an understanding of how this would improve their well-being. Imbursement of workers for clearing and implementing restoration treatments enabled them to buy groceries and clothes, and to take care of other basic needs. One participant from the Shongoane area even said that the remuneration contributed towards completing a building project. In terms of satisfaction with compensation for participation in the programme, women aged 25 years and above were more satisfied with the remuneration. Of interest here is that male participants in the age group 22–35 years complained that the remuneration they received was not sufficient to cover their needs in general.

Participants at the D'Nayala NR expressed that the project was beneficial since it provided employment and increased the livelihoods of the community surrounding the nature reserve. Eco-tourism also benefitted from the clearing/controlling of the dense woody species as it improved visibility in the nature reserve (De Klerk 2004; Arbieu et al. 2017).

Conclusion

The results showed that BP restoration treatments increased the grass biomass production over a two-year period. Increased grass biomass production will favour livestock owners and small-scale land users, especially in communally managed areas that are characterised by BT. The results show that the density of especially the perennial grasses improved in the plots where the BP restoration methods were applied especially in the Shongoane and D'Nyala sites. The grazing capacity should further improve over time if the BP restoration plots are maintained.

The volumetric soil moisture content was higher at deeper soil depths (20–30 cm) than in the shallower 0–10 cm surface soil for all study sites, but could not be linked to BP. This was especially evident at Shongoane and could be attributed to the higher clay content of the soils. The results show that, in the short term, soil type has a larger effect on the soil moisture content after restoration. More research over a longer time period is needed to determine if the soil moisture differences at the two depths sampled will occur due to BP, especially at the Shongoane and Manthe study sites.

The overall impression of the participants with regards to the restoration project to control BT was positive, as it did not only provide an income and increase in the grazing capacity for their livestock after restoration was carried out, but also made the people aware of land degradation and the value of their land. Participants at the D'Nayala NR expressed that the restoration project was beneficial since it provided employment and increased the livelihoods of the community surrounding the nature reserve and also improved game viewing.

Participants showed appreciation for the cost-effective BP method especially after witnessing the positive results of grass biomass increase. The easy implementation of the BP methodology and the contribution to the well-being of the people was evident. It must be emphasised that only if this restoration method is maintained, will it have a positive impact on the SLM practices over the long term. Community members must therefore be encouraged to continue with the brush packing over larger areas seeing that it can help them increase the grazing capacity for the livestock in the region. Furthermore, since the implementation of effective BP methods can improve the livelihood of affected communities due to improved financial status, this method should be considered by both decision-makers and land users as a viable option to counter BE and BT.

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Authors contributions

All the co-authors are thanked for their valuable contributions regarding the research and experiments carried out for the project, calculations after experiments and to write the manuscript. KK planned and coordinated the study, and wrote the manuscript in collaboration with HC, RM, TS and NM who collected field data and conducted data analyses, all from the North-West University. JC helped with the supervision and statistical analysis (Agricultural Research Council). PM and JK, both from the North-West University, acted as co-supervisors for post-graduate studies.

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Effects of land-use change on herbaceous vegetation in a semi-arid Mopaneveld savanna

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Background: Low altitude Mopaneveld savanna in the northeastern parts of South Africa is generally well conserved. However, extensive copper mining, agricultural practices and urbanisation in the Phalaborwa region prompted research on the possible effects of land-use change on plant community diversity and function. Species diversity measures are usually considered adequate to assess disturbance effects to inform conservation efforts and management practices. However, diversity measures based on species level accounts often limit the outcomes of these studies as this approach fails to quantify how disturbances affect ecosystem functioning when community assembly, and not species diversity alone, is altered by land-use change.

Objectives: The aim of this study was to apply both species and functional diversity measures to a data set derived from various land-use types (i.e. areas exposed to strip mining activities, communal farming practices and conservation) in the Phalaborwa region to examine the effects of land-use change on the community ecology of the herbaceous layer.

Results: Land-use change, particularly severe top-soil disturbances through strip mining activities, had a significant filtering effect on all measures of species diversity, though functional evenness was maintained across land-use types.

Conclusion: These results suggest that, despite initial species loss, this particular savanna ecosystem is buffered against anthropogenic disturbances through functional stability. Indicator species analyses, as well as relationships between plant functional types and land-use change, revealed that forb species are largely responsible for ecosystem stability in areas exposed to anthropogenic disturbances.

Keywords: forb, plant functional type, anthropogenic disturbances, ecosystem stability

Introduction

Global land-use intensification and non-sustainable land-use practices are pushing terrestrial biomes beyond their environmental boundaries (Newbold et al. 2015), resulting in biodiversity losses. Increasing land-use pressure in African savannas has led to significant species loss (e.g. Shackleton 2000; Rutherford, Powrie & Thompson 2012; Zerbo et al. 2016). Since savannas provide essential ecosystem goods and services to indigenous livelihoods (Shackleton 2000), decreasing species richness and abundances that approach global thresholds (Newbold et al. 2015) should be of great concern in Africa.

Reducing biodiversity loss requires larger protected areas, land-use diversification or active restoration of degraded landscapes (Newbold et al. 2015; Dudley et al. 2018). Protected areas function to counter species loss as they are designed to maintain habitat integrity and species diversity. However, higher species richness is often reported in landscapes outside protected areas

(Shackleton 2000), often in areas perceived as degraded due to habitat transformation associated with severe anthropogenic pressure. For instance, communal rangelands are generally associated with lower plant cover (Shackleton 2000; Rutherford, Powrie & Thompson 2012), but species richness, diversity and evenness can either be maintained (Rutherford, Powrie & Thompson 2012) or enhanced (Shackleton 2000) under high intensity communal grazing. Other studies on grazing effects on plant communities state that species richness and diversity alone seem to have weak responses to increasing grazing pressure (Hanke et al. 2014; Herrero-Jáuregui & Oesterheld 2018). Further weaknesses in studying disturbance effects on vegetation include a limited understanding of the relationship between diversity patterns and plant functional attributes, especially in African savannas. Linking plant species diversity and abundance patterns to functional trait groups and trait diversity should elucidate the potential vulnerability of African savannas to anthropogenic drivers of ecosystem change and improve our understanding of African savanna ecosystem resilience (Hanke et al. 2014; Osborne et al. 2018).

Relating biodiversity and functional losses to current land-use practices (Botha et al. 2017) should consider the intensity, and more specifically the duration of land-use disturbances, since past effects strongly affect biodiversity patterns and resilience (Shackleton 2000). This study therefore aimed to test land-use change effects on the community ecology of herbaceous vegetation in a semi-arid Mopaneveld savanna, with the specific objectives to (i) consider context-specific disturbance effects, and (ii) compare species- and functional trait responses across land-use types, in this case strip mines, communal land and protected area. Context-specific disturbance effects consider the species pool, and how long and intense the area has been exposed to a particular disturbance.

Land-use practices can be classified into land-use classes (Scholes & Biggs 2005). Mining sites are included under the urban land-use class, whereas communal areas of varying land-use intensity are considered to represent a degraded land-use class. Protected areas, without any clear, direct anthropogenic disturbances, fall under the protected land-use class. We expected that the herbaceous vegetation in the protected land-use class, which is adapted to natural disturbances such as herbivory, fire and climate variability, will host highest species and functional diversity (Gray et al. 2016). Increased herbaceous species richness in communal rangelands (Shackleton 2000; Rutherford, Powrie & Thompson 2012) led us to predict highest richness, diversity and evenness (at both species and functional trait levels) in the degraded land-use class. In contrast, we expected lowest species richness, diversity and evenness in the mining sites (i.e. urban land-use class) due to extensive soil disturbances at these sites (Yan, Zhao & Sun 2013). Herbaceous plant functional types were predicted to represent adaptations to competition (e.g. in the protected, untransformed area), abiotic limitation (e.g. in transformed, mining areas) or periodic biomass destruction (e.g. in the degraded communal areas) (Shackleton 2000; Hillebrand, Bennet & Cadotte 2008). An improved understanding of the community ecology of herbaceous vegetation across land-use types will indicate how species and their respective functions are affected by land-use changes, and how they can be maintained under increasing land-use pressure and drought (Siebert & Dreber 2019; Siebert, Klem & Van Coller 2020; Kellner et al. 2021).

Methods

Site description

The study was conducted in the Phalaborwa region (23°56′45.47′′S; 31°08′46.23′′E) of Limpopo, South Africa (Figure 1). The Phalaborwa–Timbavati Mopaneveld is characterised by an undulating, open tree savanna landscape dominated by the leguminous tree *Colophospermum mopane* (J.Kirk ex Benth.) J.Kirk ex J.Léonard (Mucina & Rutherford 2006). Semi-arid Mopaneveld vegetation is characterised by a homogenous woody plant structure interspersed with a dynamic herbaceous layer (Siebert, Eckhardt & Siebert 2010).

The Phalaborwa region is considered a multi-functional landscape with land-uses varying from subsistence and commercial farming, large mining operations and land managed for conservation. Considering the increases in human-induced transformation of Phalaborwa–Timbavati Mopaneveld vegetation through mining operations and human settlements (Mucina & Rutherford 2006), study sites related to these practices were selected to investigate vegetation responses. Based on the classification of Scholes and Biggs (2005), three land-use classes were sampled, which included urban (i.e. strip mining practices at Pompeye), protected (i.e. untransformed Mopaneveld) and degraded (i.e. communal rangelands and crop fields of Lulekani) (Table 1).

Strip mining is described as surface mining where vegetation, topsoil and rock material located above the targeted seam layer (i.e. quartz-feldspar) is removed (Hustrulid 2013). Two surface mined areas (land-use types) were included for this study and consisted of strips that were mined between 1970 and 1980 (>30 years since impact) and an area mined between 1995 until 2005 (i.e. more recent strips; <15 years since impact). After mining was completed, the overburden was redistributed across the mined landscape, and then shaped. Human intervention was limited and managed as part of a game reserve, which hosts several roaming game species. Vegetation was left to regenerate naturally,

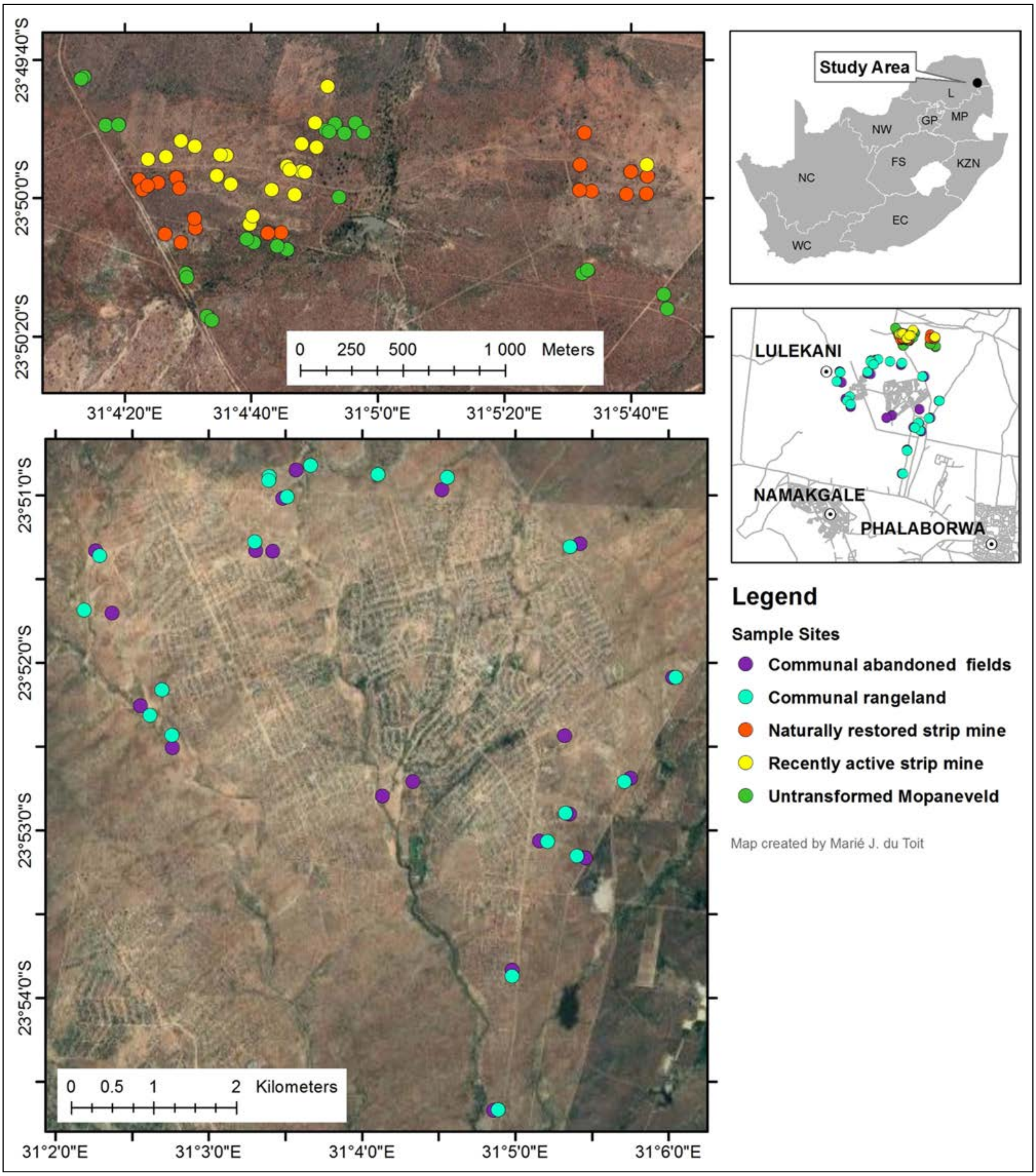

Figure 1. Study area and locality of sampled sites. Strip mines and untransformed Mopaneveld is located at Pompeye (top) and communal areas at Lulekani (bottom).

with the mined area supporting a dense grass sward and bush clumps along drainage lines. Vegetation without considerable soil disturbance or heavy grazing were selected from undisturbed parts of the reserve to serve as a benchmark system, i.e. the untransformed Mopaneveld land-use type (Table 1).

Communal areas were selected in and around the rural communal village of Lulekani, approximately 5 km west of strip-mined and untransformed sites at Pompeye. This degraded land-use class (Scholes & Biggs 2005) has a long history of subsistence farming, including small-scale crop fields and communal rangelands. Subsistence croplands were exposed to topsoil disturbance through ploughing, although fields were not cultivated annually. Surveys were conducted in abandoned fields that have lain bare for one or more seasons. These sites were characterised by a dense herbaceous layer of

Table 1. Summary of study sites, land-use types and the respective land-use classes

Study site	Land-use types	Description of natural and anthropogenic disturbance types	Land-use class
Pompeye	Naturally restored strip mines (i.e. strip mining activity >30 years ago)	Mined between 1970 and 1980 Grazing area for game	Urban
	Recent strip mine activity area (i.e. strip mining activity <15 years ago)	Mined between 1995 and 2005 Grazing area for game	Urban
	Untransformed Mopaneveld	Managed as a game reserve Grazing area for game	Protected
Lulekani	Communal rangelands	Grazing area for livestock Heavily utilised for natural resources	Degraded
	Communal abandoned fields	Disturbed by ploughing Fields not cultivated annually Grazing area for livestock	Degraded

forbs and grasses, which were heavily grazed upon by cattle and goats that maintained the herbaceous community in a grazing lawn state (Fox et al. 2015). Shallow erosion gullies were observed. Rangelands were used as grazing areas for livestock and heavily utilised for the harvesting of natural resources, such as firewood, fruit, thatch grass and construction wood (Shackleton 2000). Resprouting trees were a common phenomenon in rangelands, whereas the abandoned fields were characterised by large, solitary specimens of large savanna trees, mostly marula (*Sclerocarya birrea* (A.Rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro).

Data collection

Floristic data were collected from February to March 2013 during the peak growing season and the ideal time during which the majority of species will be observable for diversity studies. Surveys were conducted in randomly placed sites containing pairs of 1 m^2 plots situated 50 m apart. A minimum of 20 plots per land-use were sampled to meet the optimum number for statistical analyses. All herbaceous individuals rooted within each plot were counted and identified to species level, and percentage cover of grasses and forbs (i.e. non-graminoid, dicotyledonous and monocotyledonous herbaceous plants) was visually estimated.

To elucidate potential indirect effects of woody density (in addition to land-use type) on herbaceous composition, woody vegetation was sampled along ten transects of 50 × 5 m per land-use type, following the strip transect method (Hill 2005). All trees and shrubs of >1.5 m in height within the transect were measured, namely the canopy height, stem diameter at breast height (i.e. DBH at ~1.4 m) and crown diameter. Stem diameter was converted to basal area in m^2/ha.

Species names follow Germishuizen and Meyer (2003). Unknown specimens were identified by the Pretoria National Herbarium (PRE) and voucher specimens were deposited in the A.P. Goossens Herbarium (PUC) and Skukuza Herbarium (KNP).

Data analysis

Herbaceous species composition

To assess land-use effects on herbaceous species composition, the Bray-Curtis similarity measure was selected in a Non-parametric Permutational Multivariate Analysis of Variance (PERMANOVA; permutations = 999; type III sum of squares) design (Anderson & Walsh 2013). Since rare species may add noise to community assemblage data analyses, species with an abundance value of ten or less individuals were omitted to reduce the number of statistical outliers (Lepš & Šmilauer 2003). Abundance data were fourth root transformed to furthermore reduce the weighting of abundant species. To assess the significance of clustering among land-use sites, posteriori pairwise comparison of levels of a single factor (i.e. land-use) were conducted (Anderson & Walsh 2013). Homogeneity of dispersion was tested with PERMDISP (Anderson, Ellingsen & Clark 2006). PERMDISP tests were conducted using deviations from the centroid with 9999 restricted permutations selected. Land-use type effects on herbaceous species composition were depicted by Non-metric Multidimensional Scaling (NMDS) based on the Bray-Curtis Similarity Index for ordination. PERMANOVA and PERMDISP (using the PERMANOVA PLUS routine) as well as NMDS analyses were performed in PRIMER 6 (2012) with land-use type as fixed effects.

Herbaceous species diversity

Species richness (*S*) and diversity index values were calculated in PRIMER 6 (2012) using total species richness per plot. Indices selected for further analyses were

Margalef's species richness (*d*), Pielou's evenness (*J'*) and Simpson Diversity ($1-\lambda$). Effects of land-use on richness and diversity were tested by using a hierarchical Linear Mixed Model (LMM) with plots nested within land-use types. Data not normally distributed, were transformed with the natural logarithm (Ln(x+1)). Land-use was set as a fixed factor and plots as the random factor. Type III Sum of Squares was performed to test whether land-use had a significant effect on diversity index values. Significant differences between land-use types were tested through the application of linearly independent pairwise comparisons among estimated marginal means using the Sidak multiple comparisons test. SPSS version 25 (IBM Corp, 2016) was used for LMM analyses.

Pearson's correlations (*r* coefficient) were applied to all herbaceous species diversity measures to test for indirect effects of woody density on herbaceous plant diversity and biomass.

Herbaceous indicator species and plant functional analyses

Indicator species analysis combines the relative abundance and frequency of species among sites (Dufrêne & Legendre 1997). Species with a high indicator value are therefore considered to be abundant and diagnostic of a specific treatment and/or habitat (Roberts 2019). The Indicator Value index (IndVal) was used to identify herbaceous indicator species per land-use class to improve our understanding of species-specific responses of herbaceous communities to environmental perturbations (Linstädter et al. 2014). Indicator values were calculated using the labdsv package (Dufrêne & Legendre 1997) in RStudio. Significance levels were set at $p < 0.05$.

Plant traits were assigned to each recorded species according to field guides and taxonomic literature (e.g. Germishuizen 1997; Germishuizen & Meyer 2003; Van Oudtshoorn 2009; JSTOR 2015). Traits were selected to represent tolerance or adaptability of species to anthropogenic and/or natural disturbances (Mori, Farukawa & Sasaki 2013). A complete species-trait list is provided in the supplementary material (Table S1).

All herbaceous plant species represented by more than ten individuals in at least one of the land-use classes (communal, protected and urban) were considered for functional analyses (Peco et al. 2012). The complete functional trait data matrix consisted of 202 species and seven traits. The trait–species matrix was multiplied with the species–abundance matrix using the MMult function in Microsoft Excel 2007 to produce a matrix from which trait diversity index calculations (richness, evenness and diversity) could be conducted in PRIMER 6 (Hanke et al. 2014). Similar to species diversity analyses, the effect of land-use on trait diversity index values was examined using LMM analysis in SPSS (IBM Corp 2016).

Since life history remains the strongest indicator of disturbance (Pérez-Harguindeguy et al. 2013), effects of underlying important disturbance traits may be weakened when all functional plant groups are analysed collectively (Lavorel et al. 1997). For this reason, we applied Principal Co-ordinate Analysis in PRIMER 6 (2012) of the complete species–trait matrix to test for clustering based on life history, which was confirmed by the separation of annuals and perennials in ordinal space (Figure S1). Furthermore, disturbance responses are often irregular among different herbaceous life forms (Van Coller et al. 2018). To disentangle all the plant functional types (PFTs) from the herbaceous communities in the study area, trait datasets were therefore analysed separately for annuals and perennials, of which each were further subdivided into grasses and forbs to reveal four overall functional groups. The use of binary and categorical data motivated the selection of a modified Gower dissimilarity metric (Botta-Dukát 2005) for hierarchical cluster analysis (PRIMER 6 2012). We applied UPGMA-cluster analyses (Unweighted Pair Group Method with Arithmic Mean) together with a Similarity Profile (SIMPROF) test to identify clusters. SIMPROF is described as an objective method for the identification of significant groupings compared to subjective cut-off levels (Clarke, Somerfield & Gorley 2008). Groupings of plant functional groups were therefore identified by the cut-off point, indicated by SIMPROF where dashed lines within the dendrogram denoted no significant groupings. Each life history group was analysed separately to identify, describe and discuss the PFTs across land-use types. Plant functional trait (PFT) clusters were identified according to the grouping of plant species based on their trait scores, which revealed PFTs at different hierarchical levels, following the approach of Linstädter et al. (2014). A Principal Component Analysis, using CANOCO 5 software (Šmilauer & Lepš 2014), was applied to the data to provide a summary of community trait variation and to investigate to what extent the PFTs that were correlated with land-use types.

Results

Herbaceous species composition

PERMANOVA results revealed a significant effect of land-use on herbaceous species composition (*Pseudo-F* = 5.703; $p < 0.001$), although the two-dimensional visual representation of the ordination (NMDS) showed rather weak clustering of plots according to land-use types (Figure 2). Homogeneity of multivariate dispersion was not significant among the communal land-use types and the protected area ($F = 0.662$; $p = 0.52$), which support the significance of clustering of these land-use types. Therefore, herbaceous species composition of the communal land-use types in our study area differed significantly from the untransformed protected

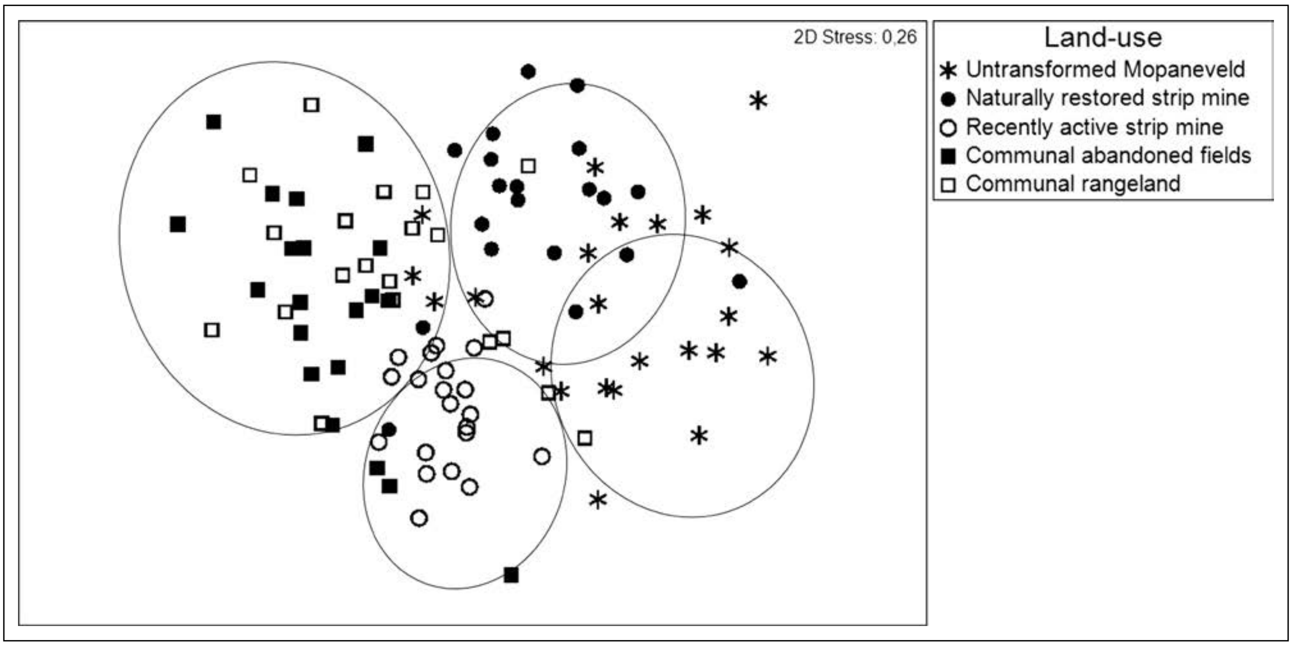

Figure 2. Multidimensional Scaling (NMDS) ordination of sampling plots representing herbaceous species assemblages across land-use types. Broad groupings are encircled.

area ($p < 0.001$; $t > 2$). Species composition of the two communal land-use types (i.e. communal rangeland and communal abandoned fields) was not significantly distinct ($p = 0.099$; $t < 2$).

Multivariate data dispersion of the strip mining and protected area land-use types was, however significant ($F = 18.86$; $p < 0.001$). Significant differences in species composition among the two strip mining types ($p < 0.001$; $t = 4.23$) and the untransformed protected area site ($p < 0.001$; $t < 2$), should therefore be interpreted with caution. However, since the recently active strip mining site was exposed to the most recent soil disturbance, it can be expected that species composition in this site may be dominated by a suite of species and traits that are quite distinct from more heterogeneous sites, such as the untransformed protected area site and the naturally restored strip mining site.

Woody density

The mean woody density, dominated by *C. mopane*, was highest in the untransformed site (22 378 m^2 ha^{-1} ± 14 595), and higher than the recently active strip mine area (2 726 m^2 ha^{-1} ± 3 590) and communal rangeland (4 572 m^2 ha^{-1} ± 9 893). *Dichrostachys cinerea* (L.) Wight & Arn., and not *C. mopane*, dominated the woody layer in the transformed land-use types. Since woody density did not correlate with increases or decreases in herbaceous species diversity or biomass (Pearson's correlation coefficient ($-0.5 < r < 0.5$) for both variables), herbaceous vegetation changes are assumed to more strongly reflect effects of land-use changes than of local-scale woody density.

Indicator species

The protected area and the communal abandoned fields hosted the highest richness in indicator species (16 and 18 species respectively). Communal rangelands and recently active strip mines hosted only six indicator species (IndVal >0.12; $p < 0.05$) of which the majority were annual forbs (rangelands) or annual grasses (strip mine) (Table 2). Forbs represented 50% of all indicator species in the protected area and increased to over 80% in the naturally restored strip mine, communal rangelands and abandoned fields (Table 2). The abandoned fields in the communal area hosted the most alien indicator species, which included *Acanthospermum hispidum* DC., *Boerhavia cordobensis* Kuntze, *Gomphrena celosioides* Mart. and *Schkuhria pinnata* (Lam.) Cabrera., although none of these are considered to be alien invasive species. The only two indicator grass species on the abandoned fields were the palatable *Sporobolus ioclados* (Trin.) Nees and *Urochloa panicoides* P.Beauv., whereas the communal rangeland indicator grass, *Tragus berteronianus* Schult. (Table 2), is an annual, disturbance-tolerant species. The recently active strip mine was dominated by the perennial grass *Urochloa mosambicensis* (Hack.) Dandy. This indicator germinates rapidly from seed in areas prone to soils disturbance. Considering life history, perennial indicator species were favoured by protected and naturally restored land-use types, which also hosted the highest richness in plant families among indicator species (Table 2).

Species and trait diversity

Land-use type had a significant effect on all measures of herbaceous species richness and diversity (Table 3).

Table 2. Results of indicator species analysis based on mean herbaceous species counts at the four land-use types in a semi-arid Mopaneveld savanna. Indicator values (IndVal) are accompanied by a p-value based on permutation tests. Only species with a significant indicator value ($p<0.05$) are presented

Family	Species	Grass/forb	Life history	IndVal	p-value
Protected Mopaneveld					
Malvaceae	*Hibiscus micranthus* L.f.	Forb	Perennial	0.46	0.001
Fabaceae	*Rhynchosia minima* (L.) DC.	Forb	Perennial	0.35	0.001
Poaceae	*Panicum maximum* Jacq.	Grass	Perennial	0.31	0.002
Acanthaceae	*Ruellia cordata* Thunb.	Forb	Perennial	0.3	0.002
Poaceae	*Chloris roxburghiana* Schult.	Grass	Perennial	0.25	0.002
Poaceae	*Bothriochloa radicans* (Lehm.) A.Camus	Grass	Perennial	0.23	0.002
Fabaceae	*Indigofera nebrowniana* J.B.Gillett	Forb	Perennial	0.22	0.003
Fabaceae	*Chamaecrista absus* (L.) Irwin & Barneby	Forb	Annual	0.2	0.012
Poaceae	*Aristida scabrivalvis* Hack.	Grass	Annual	0.19	0.017
Euphorbiaceae	*Tragia rupestris* Sond.	Forb	Perennial	0.17	0.014
Sterculiaceae	*Melhania acuminata* Mast.	Forb	Perennial	0.17	0.006
Euphorbiaceae	*Acalypha indica* L.	Forb	Annual	0.16	0.04
Verbenaceae	*Lantana rugosa* Thunb.	Forb	Perennial	0.16	0.013
Boraginaceae	*Heliotropium ciliatum* Kaplan	Forb	Perennial	0.13	0.028
Convolvulaceae	*Ipomoea sinensis* (Desr.) Choisy	Forb	Annual	0.13	0.05
Poaceae	*Themeda triandra* Forssk.	Grass	Perennial	0.13	0.035
Naturally restored strip mines (>30 years)					
Amaranthaceae	*Kyphocarpa angustifolia* (Moq.) Lopr.	Forb	Annual	0.45	0.001
Fabaceae	*Indigofera vicioides* Jaub. & Spach	Forb	Perennial	0.38	0.001
Euphorbiaceae	*Phyllanthus parvulus* Sond.	Forb	Perennial	0.28	0.006
Poaceae	*Melinis repens* (Willd.) Zizka	Grass	Annual	0.24	0.002
Malvaceae	*Hibiscus sidiformis* Baill.	Forb	Annual	0.24	0.007
Poaceae	*Heteropogon contortus* (L.) Roem. & Schult.	Grass	Perennial	0.22	0.007
Violaceae	†*Hybanthus enneaspermus* (L.) F.Muell.	Forb	Perennial	0.2	0.002
Amaranthaceae	†*Achyranthes aspera* L.	Forb	Perennial	0.2	0.009
Convolvulaceae	*Seddera suffruticosa* (Schinz) Hallier f.	Forb	Perennial	0.16	0.045
Euphorbiaceae	*Euphorbia neopolycnemoides* Pax & K.Hoffm.	Forb	Annual	0.12	0.047
Recently active strip mines (<15 years)					
Poaceae	*Urochloa mosambicensis* (Hack.) Dandy	Grass	Perennial	0.59	0.001
Euphorbiaceae	*Phyllanthus incurvus* Thunb.	Forb	Perennial	0.47	0.001
Poaceae	*Aristida adscensionis* L.	Grass	Annual	0.32	0.026
Poaceae	*Chloris virgata* Sw.	Grass	Annual	0.28	0.007
Poaceae	*Aristida bipartita* (Nees) Trin. & Rupr.	Grass	Annual	0.25	0.014
Asteraceae	*Dicoma tomentosa* Cass.	Forb	Annual	0.19	0.031
Communal abandoned fields					
Portulacaceae	*Portulaca hereroensis* Schinz	Forb	Annual	0.46	0.001
Amaranthaceae	†*Gomphrena celosioides* Mart.	Forb	Perennial	0.39	0.001
Acanthaceae	*Blepharis integrifolia* (L.f.) E.Mey. ex Schinz	Forb	Perennial	0.39	0.001

Table 2. Results of indicator species analysis based on mean herbaceous species counts at the four land-use types in a semi-arid Mopaneveld savanna. Indicator values (IndVal) are accompanied by a p-value based on permutation tests. Only species with a significant indicator value ($p<0.05$) are presented (continued)

Family	Species	Grass/forb	Life history	IndVal	p-value
Communal abandoned fields (continued)					
Tiliaceae	*Corchorus confusus* Wild	Forb	Perennial	0.34	0.036
Molluginaceae	*Hypertelis bowkeriana* Sond.	Forb	Perennial	0.26	0.002
Portulacaceae	*Portulaca trianthemoides* Bremek.	Forb	Annual	0.26	0.005
Polygonaceae	*Oxygonum sinuatum* (Hochst. & Steud. ex Meisn.) Dammer	Forb	Annual	0.23	0.014
Nyctaginaceae	†*Boerhavia cordobensis* Kuntze.	Forb	Annual	0.21	0.005
Poaceae	*Sporobolus ioclados* (Trin.) Nees	Grass	Perennial	0.2	0.005
Gisekiaceae	*Gisekia africana* (Lour.) Kuntze	Forb	Annual	0.17	0.013
Molluginaceae	*Limeum dinteri* G.Schellenb.	Forb	Perennial	0.16	0.021
Pedaliaceae	*Ceratotheca triloba* (Bernh.) Hook.f.	Forb	Annual	0.16	0.015
Poaceae	*Urochloa panicoides* P.Beauv.	Grass	Annual	0.15	0.042
Asteraceae	†*Acanthospermum hispidum* DC.	Forb	Annual	0.15	0.016
Asteraceae	†*Schkuhria pinnata* (Lam.) Cabrera	Forb	Annual	0.15	0.025
Sterculiaceae	*Hermannia boraginiflora* Hook.	Forb	Perennial	0.15	0.028
Fabaceae	*Crotalaria distans* Benth.	Forb	Annual	0.13	0.023
Fabaceae	*Crotalaria steudneri* Schweinf.	Forb	Annual	0.13	0.023
Communal rangeland					
Fabaceae	*Zornia glochidiata* DC.	Forb	Annual	0.3	0.009
Poaceae	*Tragus berteronianus* Schult.	Grass	Annual	0.24	0.028
Molluginaceae	†*Mollugo nudicaulis* Lam.	Forb	Annual	0.22	0.009
Molluginaceae	*Limeum viscosum* (J.Gay) Fenzl	Forb	Annual	0.19	0.002
Portulacaceae	*Portulaca quadrifida* L.	Forb	Annual	0.19	0.02
Acanthaceae	*Barleria senensis* Klotzsch	Forb	Perennial	0.15	0.024

† Alien plant species

The land-use type with recent (<15 years) strip mining activities was the only to reveal significant deviations from the benchmark (i.e. untransformed protected area) mean values for all diversity measures (Figure 3; $p < 0.05$). Species evenness was also significantly lower in the abandoned fields ($p = 0.018$) compared to the protected area (Figure 3).

Significant land-use type effects on trait diversity measures were revealed for total trait richness, Margalef trait richness and Simpson trait diversity (Table 3). Functional trait measures of diversity across transformed land-use types revealed weak deviations from the benchmark means (i.e. untransformed/protected area), with the exception of significantly lower Simpson trait diversity recorded for the recently active strip mining area (Figure 3; $p<0.05$). Margalef trait richness deviated significantly from the benchmark means for the abandoned fields ($p < 0.001$) and both the recently active ($p < 0.001$) and naturally restored ($p = 0.037$) strip mining sites (Figure 3). Functional trait evenness index values were almost equal to the benchmark means across all land-use types (Figure 3).

Plant functional types

Cluster analyses assisted in the identification of 21 plant functional types (PFT's). Shade tolerance initiated the highest hierarchical separation in annual grasses (PFT 1–3; Figure S2), followed by growth form, although perennial grasses (PFT 7–10; Figure S3) were strongly separated according to their ability to resprout at, or below the soil surface. Lower hierarchical clustering of perennial grasses was initiated by shade tolerance. In annual forbs (PFT 4–6; Figure S4), the first level clustering was initiated by their ability to fix nitrogen, followed by seed dispersal mode. Perennial forbs were rich in PFT's

Table 3. Linear mixed model fixed effects of land-use type on measures of diversity. Significance ($p < 0.05$) are indicated with an asterisk (*). *df*, degrees of freedom; Num., numerator; Den., denominator; SE, standard error

	df		**Residual**				**F**		**Sig**	
	Num.	**Den.**	**Estimates**		**SE**					
			Species	**Traits**	**Species**	**Traits**	**Species**	**Traits**	**Species**	**Traits**
Total richness	4	46	22.41	1.480	4.44	0.293	5.523	3.561	0.001*	0.013*
Margalef richness	4	46	0.966	0.062	0.191	0.012	7.561	13.119	<0.001*	<0.001*
Simpson diversity	4	46	0.030	<0.001	0.006	<0.001	4.366	4.879	0.004*	0.002*
Pielou evenness	4	46	0.025	0.002	0.005	<0.001	4.759	1.908	0.003*	0.125

(PFT 11–21; Figure S5) that were clustered according to their ability to resprout at or below the soil surface, ability to fix nitrogen, growth form and shade tolerance (in descending order of hierarchical levels) (Figure S4). Plant trait descriptions are presented in Table 4.

The first two axes (Principal Components) of the PCA explained 36.96% of variance observed in PFT data (Axis 1= 21.65%; Axis 2= 15.32%; Figure 4). The largest contribution of the variance within PFTs (21.65%) was explained by the first principal component (Axis 1; Figure 4), which was mainly correlated with soil disturbance, including ploughing (i.e. abandoned crop fields) and ripping (recently active strip mining area). Nitrogen-fixing annual forbs (PFT 4) and perennial forbs, with a prostrate growth form and the ability to resprout at or near the soil surface (PFT 18), were strongly correlated with abandoned crop fields of communal areas, whereas annual forbs without nitrogen-fixing abilities (PFT's 5 and 6) were associated with both types of communal land-uses (abandoned fields and rangelands). Perennial grasses growing in full sun, with a prostrate,

Table 4. Descriptive summary of plant functional groups and their respective plant functional types (PFT's)

Plant functional group	Plant functional type	Description of PFT
Annual grasses	PFT1	Annual, shade-tolerant tussock grasses
	PFT2	Annual prostrate grasses
	PFT3	Annual tussock grasses
Annual forbs	PFT4	Annual, nitrogen-fixing forbs
	PFT5	Annual, auto- or anemochorous forbs
	PFT6	Annual zoochorous forbs
Perennial grasses	PFT7	Perennial, shade-tolerant, non-resprouting grasses
	PFT8	Perennial non-resprouting grasses
	PFT9	Perennial resprouting grasses
	PFT10	Perennial, shade-tolerant, resprouting grasses
Perennial forbs	PFT11	Perennial, shade-tolerant climbers
	PFT12	Perennial, erect, shade-tolerant forbs
	PFT13	Perennial, erect forbs
	PFT14	Perennial, resprouting climbers
	PFT15	Perennial, Nitrogen-fixing, resprouting climbers
	PFT16	Perennial, Nitrogen-fixing, erect, resprouting forbs
	PFT17	Perennial, resprouting creeping forbs
	PFT18	Perennial, prostrate resprouting forbs
	PFT19	Perennial, erect, shade-tolerant, resprouting forbs
	PFT20	Perennial, erect, resprouting forbs
	PFT21	Perennial goephytes and sedges

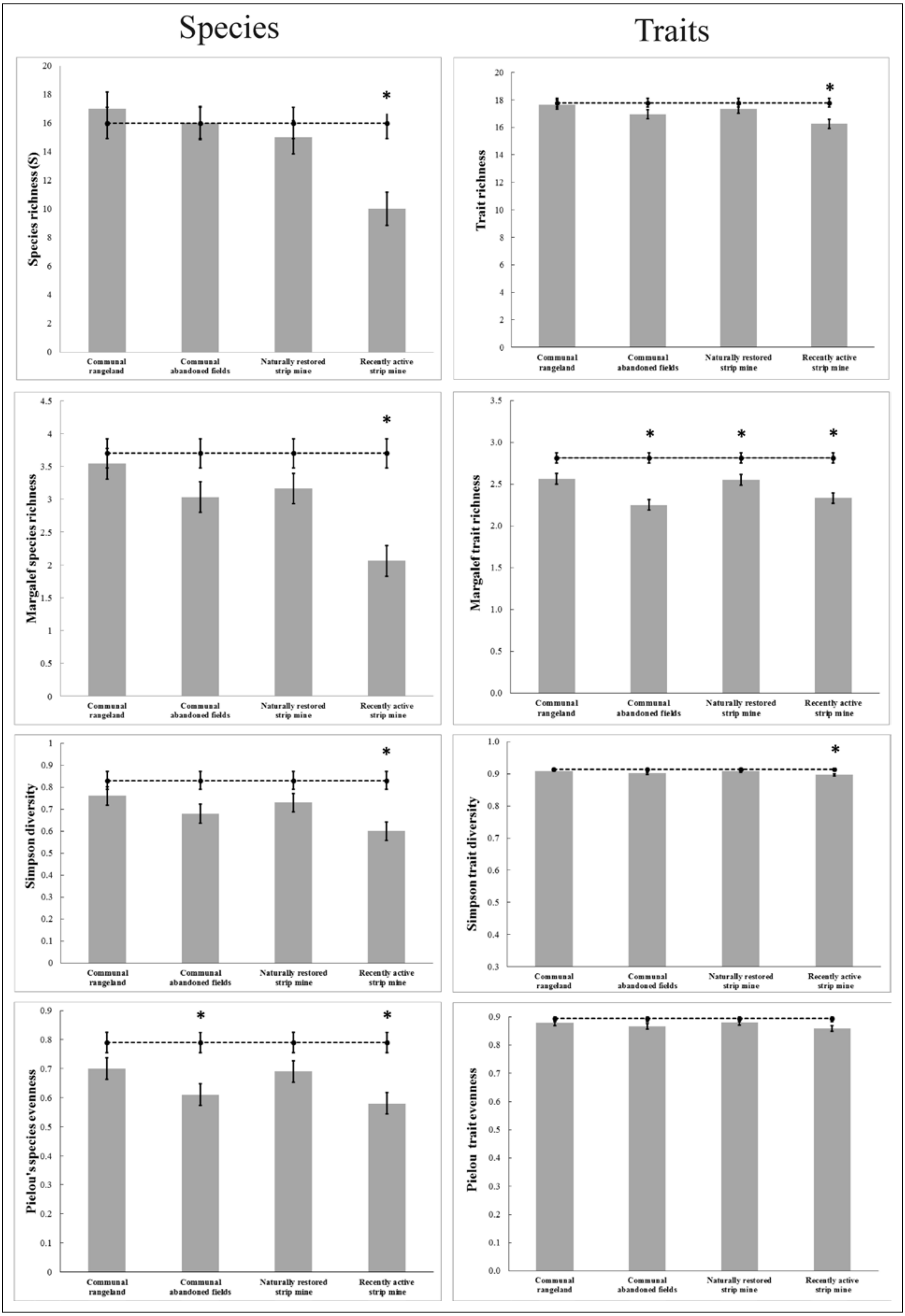

Figure 3. Herbaceous species (left) and trait (right) diversity measures benchmarked against the mean value calculated for the untransformed (protected) area (----) across transformed land-use types. Vertical bars denote 0.95 confidence intervals. Significant deviations from the protected area (Sidak posthoc pairwise comparison; $p < 0.05$) are denoted by (*).

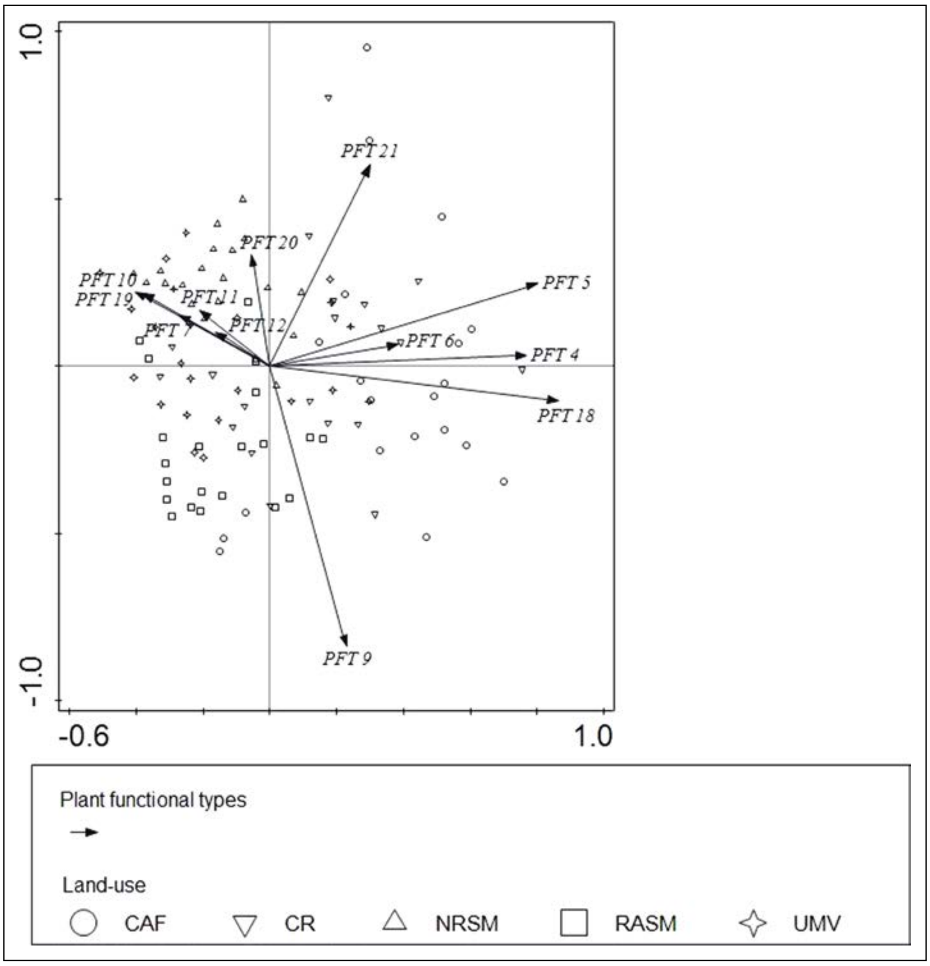

Figure 4. Principal Component Analysis (PCA) ordination of land-use type sampling plots correlated with plant functional types (PFT's). CAF (Communal abandoned fields); CR (Communal rangelands); NRSM (Naturally restored strip mine); RASM (Recently active strip mine); UMV (Untransformed Mopaneveld).

stoloniferous growth form (PFT 9) were favoured by all land-use types, except for the naturally restored strip mine, with which shade-tolerant grass and forb PFT's were correlated (PFT's 7,10,11,12–19). Perennial forbs with an erect growth form and the ability to resprout below or near the soil surface (i.e. forbs of which the stems may become lignified, but of which the woody stems are consumed by fire and/or herbivory) (PFT 20) were associated with naturally restored strip mined areas (Figure 4). There is no clear relationship between any PFT's and untransformed Mopaneveld, indicating that no PFT defines this land-use.

Discussion

Degraded land-use effects

Land-use contrasts are commonly used to analyse corresponding effects on spatiotemporal vegetation and biodiversity patterns in African savanna ecosystems. The majority of such studies have focused on the contrast between high intensity grazing in communal rangelands (perceived as degraded landscapes) opposed to protected areas (e.g. Shackleton 2000; Rutherford, Powrie & Thompson 2012; Hanke et al. 2014; Zerbo et al. 2016). Communal land-use practices with dissimilar soil disturbance histories (e.g. rangelands versus abandoned, bush-cleared croplands) were expected to display disparate herbaceous species assemblages (Hiernaux et al. 2009; Kellner et al. 2021), but this was not supported by our results. Weak negative effects of different communal land-use practices on species composition in this study suggest that long-term exposure to regular disturbances may induce tolerance to such events (Rutherford, Powrie & Thompson 2012).

The maintenance of species richness, diversity and evenness in the communal rangeland supported previous findings of Rutherford, Powrie and Thompson (2012) and Shackleton (2000). Large herbivores are known to maintain species richness and diversity through their suppressive effects on standing herbaceous biomass, albeit through grazing and browsing by wild game in protected areas (Van Coller & Siebert 2015), or by livestock in communal rangelands (Zerbo et al. 2016).

Conservation management is generally directed towards protecting species numbers as diversity may enhance temporal stability, a mechanism referred to as the insurance hypothesis (Yachi & Loreau 1999). In contrast, the effects of disrupted evenness on ecosystem stability are less explored (Crowder et al. 2010; Mori, Farukawa & Sasaki 2013). Low species evenness displayed by the abandoned fields implies dominance of a few disturbance-tolerant species, a common result of human-induced environmental degradation (Hillebrand, Bennet & Cadotte 2008; Wittebolle et al. 2009). Such communities are often more susceptible to invasion (Mason et al. 2005; Crowder et al. 2010) and are expected to be less resilient to disturbances. Indicator species analyses partially supported this hypothesis, as over 50% of the indicator species on the abandoned fields were annuals, of which the majority were alien species. Linking PFT's with land-uses supported these results as the PFT's that correlated strongly with the abandoned fields were ruderal, disturbance-adapted species, which included annual forbs, some with the ability to fix nitrogen, and perennial, prostrate forbs with the ability to resprout after disturbances such as fire, herbivory or drought stress. These results can be interpreted as yet another example of a typical trait syndrome of herbaceous plants subjected to defoliation, such as grazing (Moreno Garcia et al. 2014), although our results highlight the significance of forbs as useful indicators of potential regime shifts (Siebert & Dreber 2019).

Evidence of negative effects of communal land-use types on ecosystem stability could not be provided. Although both communal land-use types hosted a lower trait richness than the protected area, trait evenness and diversity were maintained at both sites, suggesting trait-based redundancy. Trait-based redundancy is provided through dominant stress-tolerant species with similar trait sets that contribute to functional compensation for the species that were lost from the community (Lavorel et al. 2011), a mechanism that provides ecosystem stability (Mori, Farukawa & Sasaki 2013). These findings support previous findings that functional trait diversity patterns, including evenness, better explain disturbance effects than biodiversity loss only (Vandewalle et al. 2010; Hanke et al. 2014).

Urban land-use effects

Mining activities are known to have direct and indirect effects on biodiversity through habitat destruction and soil disturbances (Yan, Zhao & Sun 2013), which may ultimately lead to diversity loss and homogenisation of plant communities if alien species colonise this land-use type (Dassonville et al. 2008). Strip mining practices did not lead to homogenisation of herbaceous plant communities since species composition among the two strip mining land-use types was quite distinct. Species composition in the recently active strip mining site differed from both the naturally restored strip mining site and the untransformed protected area. These results support the expected negative effects of topsoil disturbance on plant species composition (Lubke, Avis & Moll 1996). However, such vegetation states may be temporal, explaining heterogeneity among the strip mining land-use types, which was driven by native annual grasses as the only indicator species for the recently active mining site. Herbaceous communities on the naturally restored sites (i.e. soil disturbance which occurred over 30 years ago) hosted species assemblages comparable to the protected area. This is in accordance with results from coastal dune rehabilitation studies, where sites with a longer history of limited rehabilitation interferences revealed vegetation states comparable to unmined communities (Van Aarde et al. 1996). Moreover, as the strip mine sites were left to rejuvenate without human interference, the presence of biodiversity islands comprising patches of untransformed areas (nearby species pool) could have enhanced the recovery of species assemblages in the naturally restored strip mine site.

Contrary to the weak communal land-use effects on herbaceous community diversity, the significant effects of strip mining practices suggest strong filtering effects imposed by this land-use type. Strip mining practices are associated with topsoil disturbances, which include removal of the seed- and belowground bud banks, soil compaction, decreased soil fertility, exposure to soil erosion and increased soil temperature (Shrestha & Lal 2011). Few plant species possess all the necessary traits to tolerate such disturbances, which explains the low species and functional richness within these communities. Conservation biology literature often relates such species richness declines with similar losses in ecosystem function (e.g. Cardinale et al. 2006). However, this relationship was only evident for the strip mined areas where both species and trait losses were evident. Plant communities of communal areas were less affected by land-use intensification whereas natural recovery of mining sites was largely context-specific (i.e. disturbance type, duration and the size of the surrounding species pool) (Mayfield et al. 2010). For instance, the older strip mined areas without any re-vegetation practices since the 1980s, were able to retain their function (in terms of PFTs) in this particular ecosystem, despite their exposure to a perceived destructive event. This maintenance of ecosystem function could be explained by the presumed influx of species from the species pool in the surrounding untransformed, protected area. This implies that community processes in transformed Mopaneveld have the ability to tolerate disturbance events without direct human intervention, provided that the affected area is surrounded by natural vegetation seed sources as the soil seed bank is lost during mining.

Mining land-uses had pronounced habitat filtering effects. This was especially evident through the significant loss of functional richness and diversity in the recently active strip mined area, which is in accordance with the land-use intensification hypotheses (e.g. Pakeman 2011). Contrariwise, functional trait evenness was maintained, suggesting the lack of dominance of one or more plant traits over others in these transformed landscapes. When resource availability is assumed to be even across niche space, functional evenness reflects the optimal utilisation of resources, which suggest that higher functional evenness will decrease the opportunity for undesirable plant groups, such as invader species to fill the niche space (Mason et al. 2005). High functional evenness in urban land-use types therefore infers the maintenance of ecosystem function despite species richness declines (Mason et al. 2005), although land-use intensification will reduce functional redundancy in the long-term (Lalibarté et al. 2010).

Conclusions

Herbaceous plant communities in a South African semi-arid Mopaneveld savanna are more stress-tolerant than expected, although some non-invasive alien weeds took over the function of lost species on abandoned fields. Although species and their respective functional traits were indeed affected by land-use types, the severity of the effects varied across disturbance intensity and among response variables. Despite these varying effects on herbaceous species and functional diversity, our results suggest that ecosystem functioning in this semi-arid Mopaneveld could be maintained. Predictions on increasing frequencies and intensities of land-use and climate change may push the functioning of Mopaneveld ecosystems beyond their ecological boundaries. However, our study suggests that the current state of herbaceous communities can be maintained through continued appropriate management of multi-functional landscapes in the Phalaborwa region. These results, however, do not reflect the potential negative effects imposed by large-scale commercial agricultural practices and active mining operations in the area. For subsistence-based land-use transformation, our study supported the value of protected areas surrounding transformed land-use types, as these areas aid with natural rehabilitation of plant communities. Diversity measures that include evenness are important to detect dominance shifts in semi-arid terrestrial savanna ecosystems as it better explains ecosystem resilience than richness and diversity alone. Furthermore, our results confirmed that the assessment of land-use effects on biodiversity at species level only, may be deceptive. Results from this study reflected contrasting effects of land-use change when species-based diversity index values are compared to functional trait-based changes. Complementary biodiversity measures (i.e. species and functional measures) should be included to achieve a comprehensive assessment of land-use effects on biodiversity patterns in semi-arid ecosystems.

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Authors' contributions

FS and SJS (North-West Unversity) were the project leaders, who took the lead in writing the manuscript. NvS was responsible for data collection, analyses and reporting. DMK (North-West University) assisted with data collection, plant identifications, data management and preliminary analyses. AMS (SAEON) was responsible for the study design, student supervision and logistical support.

Disclaimer

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Supplementary material

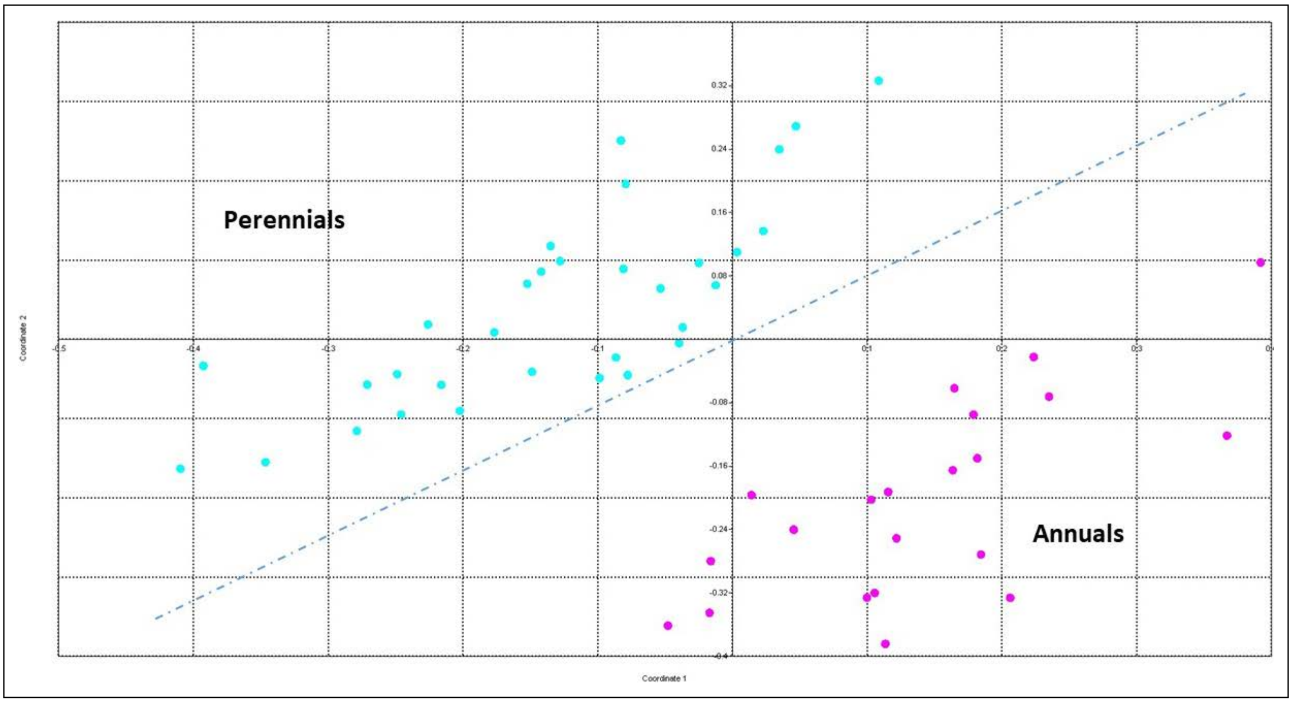

Figure S1. Principal Co-ordinate Analysis (PCoA) scatter diagram of the species-trait matrix revealing a strong clustering based on life history.

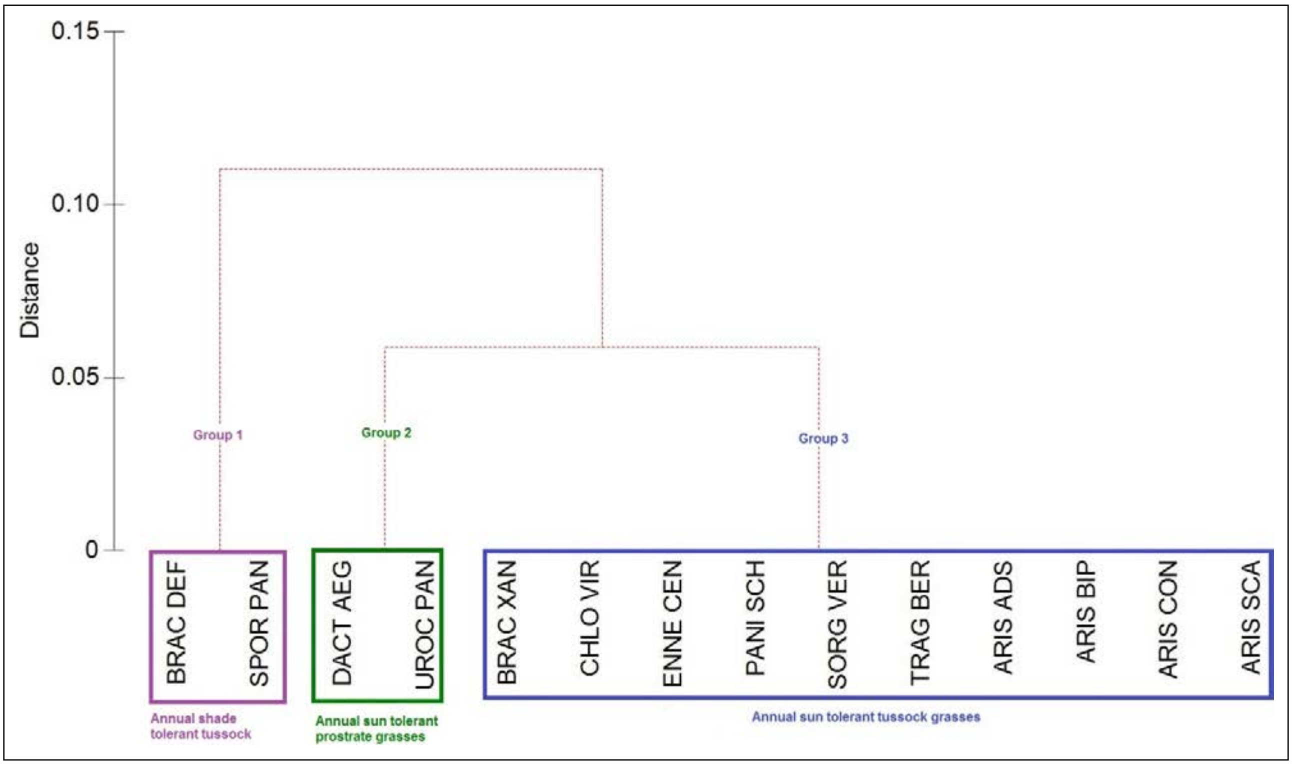

Figure S2. Unweighted Pair Group Method with Arithmetic Mean (UPGMA) based on Gower distance measure indicating annual grass plant functional types (PFTs).

Table S1. Complete species–trait list sorted by plant family. Exotic plant species are indicated by an asterisk (*)

Species	Plant family	Life form	Growth form	Clonality	Dispersal mode	Nitrogen fixing ability yes/no	Shade tolerance	Life history
Barleria lancifolia T.Anderson	Acanthaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Barleria senensis Klotzsch	Acanthaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Shade	Perennial
Blepharis integrifolia (L.f.) E.Mey. ex Schinz	Acanthaceae	Forb	Prostrate	Clonal	External animal	N-fixing ability absent	Sun	Perennial
Crabbea velutina S.Moore	Acanthaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Shade	Perennial
Justicia flava (Vahl) Vahl	Acanthaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Shade	Perennial
Justicia matammensis (Schweinf.) Oliv.	Acanthaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Shade	Annual
Justicia protracta (Nees) T.Anderson	Acanthaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Shade	Perennial
Megalochlamys revoluta (Lindau) Vollesen	Acanthaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Rhinacanthus xerophilus A.Meeuse	Acanthaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Ruellia cordata Thunb.	Acanthaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Shade	Perennial
Trianthema salsoloides Fenzl ex Oliv.	Aizoaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
**Achyranthes aspera* L.	Amaranthaceae	Forb	Erect	Non-Clonal	External animal	N-fixing ability absent	Shade	Perennial
**Alternanthera pungens* Kunth	Amaranthaceae	Forb	Prostrate	Clonal	External animal	N-fixing ability absent	Sun	Perennial
**Gomphrena celocioides* Mart.	Amaranthaceae	Forb	Prostrate	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
**Guilleminea densa* (Willd. ex Roem. & Schult.) Moq.	Amaranthaceae	Forb	Prostrate	Clonal	External animal	N-fixing ability absent	Sun	Perennial
Cyathula lanceolata Schinz	Amaranthaceae	Forb	Prostrate	Non-Clonal	External animal	N-fixing ability absent	Sun	Perennial
Hermbstaedtia odorata (Burch.) T.Cooke	Amaranthaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Kyphocarpa angustifolia (Moq.) Lopr.	Amaranthaceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Sun	Annual
Pupalia lappaceae (L.) A.Juss.	Amaranthaceae	Forb	Erect	Non-Clonal	External animal	N-fixing ability absent	Shade	Annual
Sericorema remotiflora (Hook.f.) Lopr.	Amaranthaceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Chlorophytum recurvifolium (Baker) C.Archer & Kativu	Anthericaceae	Geophyte	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Chlorpohytum galpinii (Baker) Kativu	Anthericaceae	Geophyte	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Fockea angustifolia K.Schum.	Apocynaceae	Forb	Climber	Clonal	Wind	N-fixing ability absent	Shade	Perennial
Secamone parvifolia (L.f.) J.H.Ross	Apocynaceae	Forb	Climber	Non-Clonal	Wind	N-fixing ability absent	Sun and shade	Perennial
**Acanthospermum hispidum* DC.	Asteraceae	Forb	Erect	Non-Clonal	External animal	N-fixing ability absent	Shade	Annual

Table S1. Complete species–trait list sorted by plant family. Exotic plant species are indicated by an asterisk (*) (continued)

Species	Plant family	Life form	Growth form	Clonality	Dispersal mode	Nitrogen fixing ability yes/no	Shade tolerance	Life history
**Bidens bipinnata* L.	Asteraceae	Forb	Erect	Non-Clonal	External animal	N-fixing ability absent	Sun and shade	Annual
**Schkuhria pinnata* (Lam.) Cabrera	Asteraceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Sun	Annual
**Tridax procumbens* L.	Asteraceae	Forb	Prostrate	Non-Clonal	Wind	N-fixing ability absent	Sun and shade	Annual
Calostephane divaricata Benth.	Asteraceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Sun	Annual
Dicoma tomentosa Cass.	Asteraceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Sun	Annual
Geigeria burkei Harv.	Asteraceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Litogyne gariepina (DC.) Anderb.	Asteraceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Nidorella anomala Steetz	Asteraceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Heliotropium ciliatum Kaplan	Boraginaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Heliotropium lineare (A.DC.) Gürke	Boraginaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Heliotropium strigosum Willd.	Boraginaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Cleome monophylla L.	Capparaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Commelina africana L.	Commelinaceae	Forb	Prostrate	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Commelina benghalensis L.	Commelinaceae	Forb	Prostrate	Clonal	Unassisted	N-fixing ability absent	Sun and shade	Perennial
Commelina livingstonii C.B.Clarke	Commelinaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Shade	Perennial
Convolvulus sagittatus Thunb.	Convolvulaceae	Forb	Prostrate	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Evolvulus alsinoides (L.) L.	Convolvulaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Ipomoea bolusiana Schinz	Convolvulaceae	Forb	Prostrate	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Ipomoea cairica (L.) Sweet	Convolvulaceae	Forb	Prostrate	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Ipomoea magnusiana Schinz	Convolvulaceae	Forb	Prostrate	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Ipomoea obscura (L.) Ker Gawl.	Convolvulaceae	Forb	Prostrate	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Ipomoea plebeia R.Br.	Convolvulaceae	Forb	Prostrate	Non-Clonal	Internal animal	N-fixing ability absent	Sun and shade	Annual
Ipomoea sinensis (Desr.) Choisy	Convolvulaceae	Forb	Prostrate	Non-Clonal	Internal animal	N-fixing ability absent	Sun and shade	Annual

Table S1. Complete species–trait list sorted by plant family. Exotic plant species are indicated by an asterisk (*) (continued)

Species	Plant family	Life form	Growth form	Clonality	Dispersal mode	Nitrogen fixing ability yes/no	Shade tolerance	Life history
Merremia palmata Hallier f.	Convolvulaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Seddera suffruticosa (Schinz) Hallier f.	Convolvulaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Xenostegia tridentata (L.) D.F.Austin & Staples	Convolvulaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Cucumis africanus L.f.	Cucurbirtaceae	Forb	Prostrate	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Cucumis anguria L.	Cucurbirtaceae	Forb	Prostrate	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Annual
Cucumis metuliferus E.Mey. ex Naudin	Cucurbirtaceae	Forb	Prostrate	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Annual
Cucumis zeyheri Sond.	Cucurbirtaceae	Forb	Prostrate	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Kedrostis africana (L.) Cogn.	Cucurbirtaceae	Forb	Climber	Clonal	Internal animal	N-fixing ability absent	Shade	Perennial
Bulbostylis burchellii (Ficalho & Hiern) C.B.Clarke	Cyperaceae	Sedge	Tussock	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Bulbostylis hispidula (Vahl) R.W.Haines	Cyperaceae	Sedge	Tussock	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Cyperus indecorus Kunth	Cyperaceae	Sedge	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Cyperus obtusiflorus Vahl	Cyperaceae	Sedge	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Cyperus rupestris Kunth	Cyperaceae	Sedge	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Kyllinga alba Nees	Cyperaceae	Sedge	Tussock	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Kyllinga welwitschii Ridl.	Cyperaceae	Sedge	Tussock	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Eriospermum porphyrovalve Baker	Eriospermaceae	Geophyte	Erect	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Acalypha indica L.	Euphorbiaceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Shade	Annual
Euphorbia neopolycnemoides Pax & K.Hoffm.	Euphorbiaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Phyllanthus incurvus Thunb.	Euphorbiaceae	Forb	Erect	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Phyllanthus maderaspatensis L.	Euphorbiaceae	Forb	Erect	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Phyllanthus parvulus Sond.	Euphorbiaceae	Forb	Erect	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Tragia rupestris Sond.	Euphorbiaceae	Forb	Climber	Non-Clonal	Unassisted	N-fixing ability absent	Shade	Perennial
Chamaecrista absus (L.) Irwin & Barneby	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Annual
Chamaecrista mimosoides (L.) Greene	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Annual
Crotalaria damarensis Engl.	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Annual
Crotalaria distans Benth.	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Annual
Crotalaria sphaerocarpa Perr. ex DC.	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Annual

Table S1. Complete species–trait list sorted by plant family. Exotic plant species are indicated by an asterisk (*) (continued)

Species	Plant family	Life form	Growth form	Clonality	Dispersal mode	Nitrogen fixing ability yes/no	Shade tolerance	Life history
Crotalaria steudneri Schweinf.	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Annual
Dolichos trilobus L.	Fabaceae	Forb	Climber	Clonal	Unassisted	N-fixing ability present	Sun and shade	Perennial
Indigastrum costatum (Guill. & Perr.) Schrire	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Annual
Indigofera confusa Prain & Baker f.	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Indigofera daleoides Benth. ex Harv.	Fabaceae	Forb	Prostrate	Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Indigofera filipes Benth. ex Harv.	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Indigofera heterotricha DC.	Fabaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Indigofera nebrowniana J.B.Gillett	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Indigofera rhytidocarpa Benth. ex Harv.	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Annual
Indigofera trita L.f.	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Indigofera vicioides Jaub. & Spach	Fabaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Microcharis galpinii N.E.Br.	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Annual
Rhynchosia minima (L.) DC.	Fabaceae	Forb	Prostrate	Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Rhynchosia totta (Thunb.) DC.	Fabaceae	Forb	Prostrate	Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Tephrosia purpurea (L.) Pers.	Fabaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Tephrosia rhodesica Baker f.	Fabaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Vigna unguilata (L.) Walp.	Fabaceae	Forb	Climber	Clonal	Unassisted	N-fixing ability present	Sun	Perennial
Zornia glochidiata DC.	Fabaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability present	Sun	Annual
Monsonia glauca R.Knuth	Geraniaceae	Forb	Erect	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Gisekia africana (Lour.) Kuntze	Gisekiaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Ledebouria revoluta (L.f.) Jessop	Hyacinthaceae	Geophyte	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Acrotome hispida Benth.	Lamiaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Clerodendrum ternatum Schinz	Lamiaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Leucas glabrata (Vahl) Sm.	Lamiaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Leucas sexdentata Skan	Lamiaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Ocimum americanum L.	Lamiaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial

Table S1. Complete species–trait list sorted by plant family. Exotic plant species are indicated by an asterisk (*) (continued)

Species	Plant family	Life form	Growth form	Clonality	Dispersal mode	Nitrogen fixing ability yes/no	Shade tolerance	Life history
Ocimum filamentosum Forssk.	Lamiaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Syncolostemon canescens (Gürke) D.F.Otieno	Lamiaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Abutilon austro-africanum Hochr.	Malvaceae	Forb	Erect	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Hibiscus micranthus L.f.	Malvaceae	Forb	Erect	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Hibiscus sidiformis Baill.	Malvaceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Sun	Annual
Pavonia burchellii (DC.) R.A.Dyer	Malvaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Shade	Perennial
Pavonia transvaalensis (Ulbr.) A.Meeuse	Malvaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Shade	Perennial
Sida ovata Forssk.	Malvaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
**Mollugo nudicaulis* Lam.	Molluginaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Corbichonia decumbens (Forssk.) Exell	Molluginaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Hypertelis bowkeriana Sond.	Molluginaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Limeum dinteri G.Schellenb.	Molluginaceae	Forb	Prostrate	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Limeum viscosum (J.Gay) Fenzl	Molluginaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Mollugo cerviana (L.) Ser. ex DC.	Molluginaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
**Boerhavia cordobensis* Kuntze	Nyctaginaceae	Forb	Prostrate	Non-Clonal	External animal	N-fixing ability absent	Sun and shade	Annual
**Boerhavia diffusa* L.	Nyctaginaceae	Forb	Prostrate	Non-Clonal	External animal	N-fixing ability absent	Sun and shade	Annual
**Boerhavia erecta* L.	Nyctaginaceae	Forb	Prostrate	Non-Clonal	External animal	N-fixing ability absent	Sun and shade	Annual
Ophioglossum polyphyllum A.Braun	Ophioglossaceae	Fern	Erect	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Ceratotheca triloba (Bernh.) Hook.f.	Pedaliaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
**Digitaria didactyla* Willd.	Poaceae	Grass	Prostrate	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Andropogon chinensis (Nees) Merr.	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Aristida adscensionis L.	Poaceae	Grass	Tussock	Non-Clonal	External animal	N-fixing ability absent	Sun	Annual
Aristida bipartita (Nees) Trin. & Rupr.	Poaceae	Grass	Tussock	Non-Clonal	External animal	N-fixing ability absent	Sun	Annual
Aristida congesta Roem. & Schult.	Poaceae	Grass	Tussock	Non-Clonal	External animal	N-fixing ability absent	Sun	Annual
Aristida scabrivalvis Hack.	Poaceae	Grass	Tussock	Non-Clonal	External animal	N-fixing ability absent	Sun	Annual

Table S1. Complete species–trait list sorted by plant family. Exotic plant species are indicated by an asterisk (*) (continued)

Species	Plant family	Life form	Growth form	Clonality	Dispersal mode	Nitrogen fixing ability yes/no	Shade tolerance	Life history
Bothriochloa insculpta (A.Rich.) A.Camus	Poaceae	Grass	Tussock	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Bothriochloa radicans (Lehm.) A.Camus	Poaceae	Grass	Tussock	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Brachiaria deflexa (Schumach.) C.E.Hubb. ex Robyns	Poaceae	Grass	Tussock	Non-Clonal	Internal animal	N-fixing ability absent	Shade	Annual
Brachiaria xantholeuca (Schinz) Stapf	Poaceae	Grass	Tussock	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Annual
Cenchrus ciliaris L.	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Chloris mossambicensis K.Schum.	Poaceae	Grass	Tussock	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Chloris roxburghiana Schult.	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Chloris virgata Sw.	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Sun	Annual
Cymbopogon caesius (Nees ex Hook. & Arn.) Stapf	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Cynodon dactylon (L.) Pers.	Poaceae	Grass	Prostrate	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Dactyloctenium aegyptium (L.) Willd.	Poaceae	Grass	Prostrate	Non-Clonal	External animal	N-fixing ability absent	Sun	Annual
Dactyloctenium australe Steud.	Poaceae	Grass	Prostrate	Clonal	External animal	N-fixing ability absent	Shade	Perennial
Dactyloctenium geminatum Hack.	Poaceae	Grass	Prostrate	Clonal	External animal	N-fixing ability absent	Shade	Perennial
Digitaria eriantha Steud.	Poaceae	Grass	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Enneapogon cenchroides (Roem. & Schult.) C.E.Hubb.	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Sun	Annual
Enneapogon scoparius Stapf	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Enteropogon macrostachyus (A.Rich.) Benth.	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Shade	Perennial
Eragrostis gummiflua Nees	Poaceae	Grass	Tussock	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Eragrostis lehmanniana Nees	Poaceae	Grass	Tussock	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Eragrostis nindensis Ficalho & Hiern	Poaceae	Grass	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Eragrostis rigidior Pilg.	Poaceae	Grass	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Eragrostis rotifer Rendle	Poaceae	Grass	Tussock	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Eragrostis superba Peyr.	Poaceae	Grass	Tussock	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Eragrostis trichophora Coss. & Durieu	Poaceae	Grass	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Fingerhuthia africana Lehm.	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial

Table S1. Complete species–trait list sorted by plant family. Exotic plant species are indicated by an asterisk (*) (continued)

Species	Plant family	Life form	Growth form	Clonality	Dispersal mode	Nitrogen fixing ability yes/no	Shade tolerance	Life history
Heteropogon contortus (L.) Roem. & Schult.	Poaceae	Grass	Tussock	Non-Clonal	External animal	N-fixing ability absent	Sun	Perennial
Hyperthelia dissoluta (Nees ex Steud.) Clayton	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Melinis repens (Willd.) Zizka	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Oropetium capense Stapf	Poaceae	Grass	Tussock	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Panicum coloratum L.	Poaceae	Grass	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun and shade	Perennial
Panicum deustum Thunb.	Poaceae	Grass	Tussock	Non-Clonal	Internal animal	N-fixing ability absent	Shade	Perennial
Panicum maximum Jacq.	Poaceae	Grass	Tussock	Clonal	Internal animal	N-fixing ability absent	Shade	Perennial
Panicum schinzii Hack.	Poaceae	Grass	Tussock	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Annual
Pogonarthria squarrosa (Roem. & Schult.) Pilg.	Poaceae	Grass	Tussock	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Schmidtia pappophoroides Steud.	Poaceae	Grass	Tussock	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Setaria sphacelata (Schumach.) Moss	Poaceae	Grass	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Sorghum versicolor Andersson	Poaceae	Grass	Tussock	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Annual
Sporobolus fimbriatus (Trin.) Nees	Poaceae	Grass	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Sporobolus ioclados (Trin.) Nees	Poaceae	Grass	Prostrate	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Sporobolus nitens Stent	Poaceae	Grass	Prostrate	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Sporobolus panicoides A.Rich.	Poaceae	Grass	Tussock	Non-Clonal	Internal animal	N-fixing ability absent	Shade	Annual
Themeda triandra Forssk.	Poaceae	Grass	Tussock	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Tragus berteronianus Schult.	Poaceae	Grass	Tussock	Non-Clonal	External animal	N-fixing ability absent	Sun	Annual
Tricholaena monachne (Trin.) Stapf & C.E.Hubb.	Poaceae	Grass	Tussock	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Urochloa mosambicensis (Hack.) Dandy	Poaceae	Grass	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Urochloa oligotricha (Fig. & De Not.) Henrard	Poaceae	Grass	Tussock	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Urochloa panicoides P.Beauv.	Poaceae	Grass	Prostrate	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Annual
Polygala serpentaria Eckl. & Zeyh.	Polygalaceae	Forb	Erect	Clonal	Wind	N-fixing ability absent	Sun	Perennial
Polygala sphenoptera Fresen.	Polygalaceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Sun	Annual
Oxygonum delagoense Kuntze	Polygonaceae	Forb	Prostrate	Non-Clonal	External animal	N-fixing ability absent	Shade	Annual

Table S1. Complete species–trait list sorted by plant family. Exotic plant species are indicated by an asterisk (*) (continued)

Species	Plant family	Life form	Growth form	Clonality	Dispersal mode	Nitrogen fixing ability yes/no	Shade tolerance	Life history
Oxygonum sinuatum (Hochst. & Steud. ex Meisn.) Dammer	Polygonaceae	Forb	Prostrate	Non-Clonal	External animal	N-fixing ability absent	Shade	Annual
**Portulaca oleracea* L.	Portulacaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Portulaca hereroensis Schinz	Portulacaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Portulaca quadrifida L.	Portulacaceae	Forb	Prostrate	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Portulaca trianthemoides Bremek.	Portulacaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Talinum arnotii Hook.f.	Portulacaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Agathisanthemum bojeri Klotzsch	Rubiaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Kohautia virgata (Willd.) Bremek.	Rubiaceae	Forb	Erect	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Spermacoce senensis (Klotzsch) Hiern	Rubiaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Aptosimum lineare Marloth & Engl.	Scrophulariaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Solanum delagoense Dunal	Solanaceae	Forb	Erect	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
Hermannia boraginiflora Hook.	Sterculiaceae	Forb	Prostrate	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Hermannia glanduligera K.Schum.	Sterculiaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Melhania acuminata Mast.	Sterculiaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Melhania prostrata DC.	Sterculiaceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Waltheria indica L.	Sterculiaceae	Forb	Erect	Non-Clonal	Internal animal	N-fixing ability absent	Sun	Annual
Gnidia rubescens B.Peterson	Thymelaeaceae	Forb	Erect	Non-Clonal	Wind	N-fixing ability absent	Sun	Perennial
Corchorus asplenifolius Burch.	Tiliaceae	Forb	Prostrate	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Corchorus confusus Wild	Tiliaceae	Forb	Prostrate	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Streptopetalum serratum Hochst.	Turneraceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Tricliceras glanduliferum (Klotzsch) R.Fern.	Turneraceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Annual
Tricliceras longepedunculatum (Mast.) R.Fern.	Turneraceae	Forb	Erect	Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Lantana rugosa Thunb.	Verbenaceae	Forb	Erect	Clonal	Internal animal	N-fixing ability absent	Sun	Perennial
**Hybanthus enneaspermus* (L.) F.Muell.	Violaceae	Forb	Erect	Non-Clonal	Unassisted	N-fixing ability absent	Sun	Perennial
Cissus quadrangularis L.	Vitaceae	Forb	Climber	Non-Clonal	Internal animal	N-fixing ability absent	Shade	Perennial
Tribulus terrestris L.	Zygophyllaceae	Forb	Prostrate	Non-Clonal	External animal	N-fixing ability absent	Sun	Annual

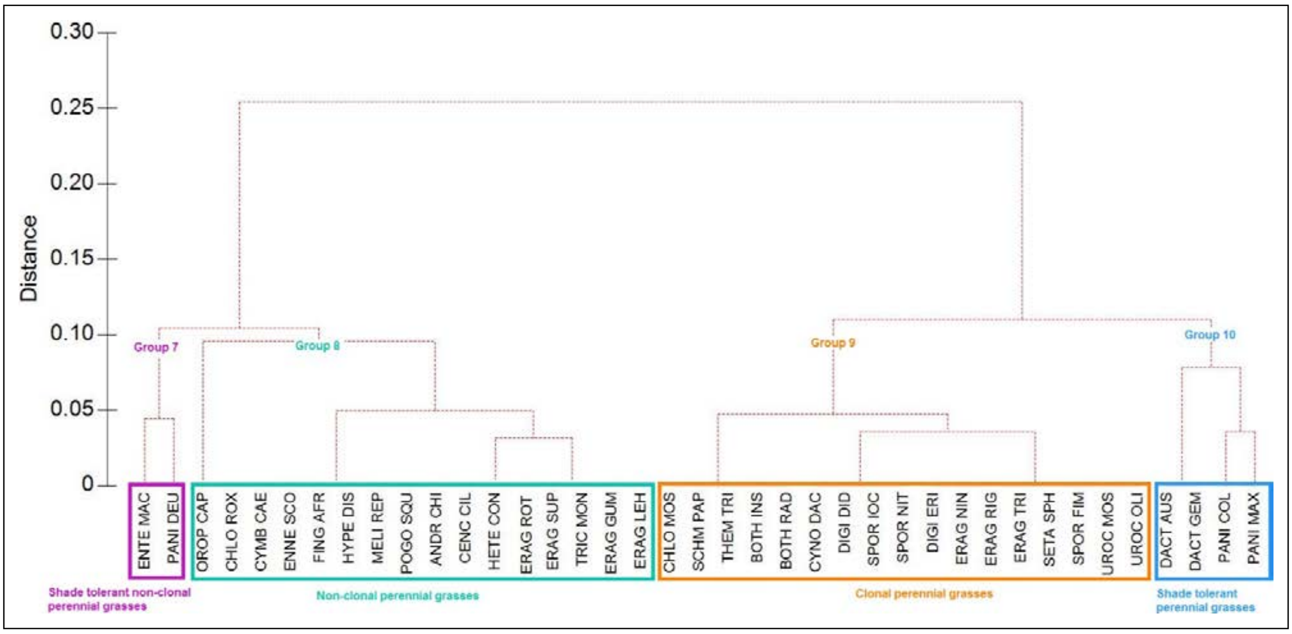

Figure S3. Unweighted Pair Group Method with Arithmetic Mean (UPGMA) based on Gower distance measure indicating perennial grass plant functional types (PFTs).

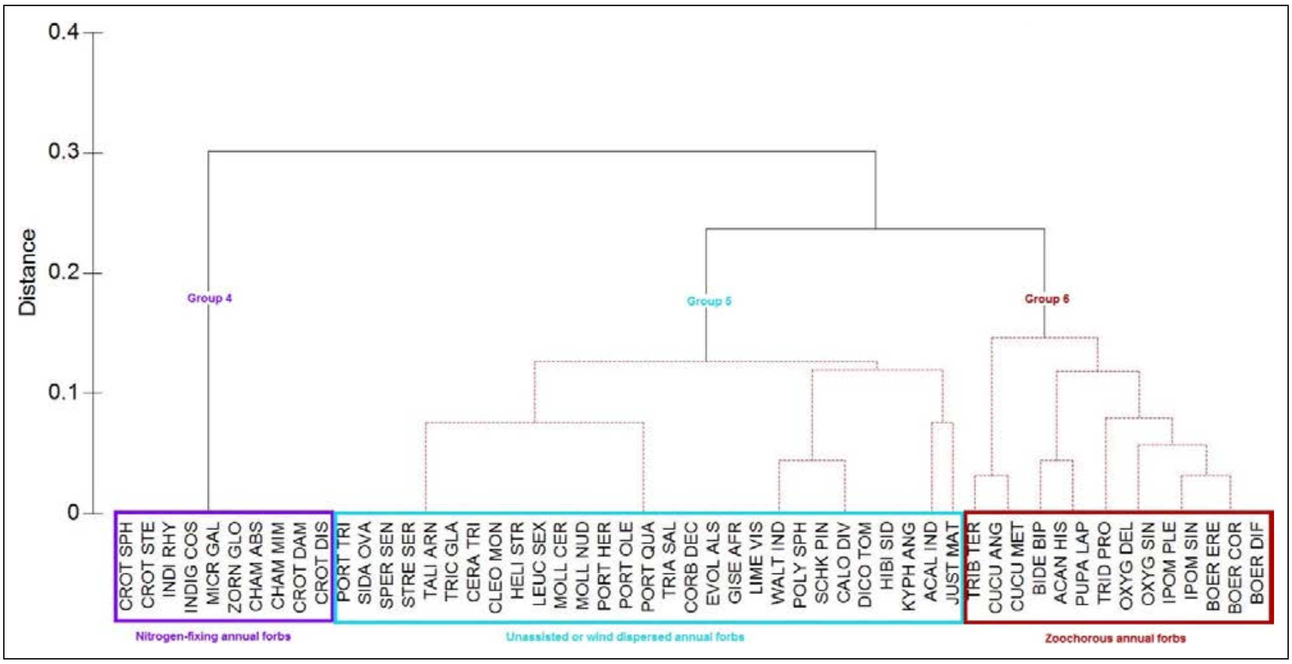

Figure S4. Unweighted Pair Group Method with Arithmetic Mean (UPGMA) based on Gower distance measure indicating annual forb plant functional types (PFTs).

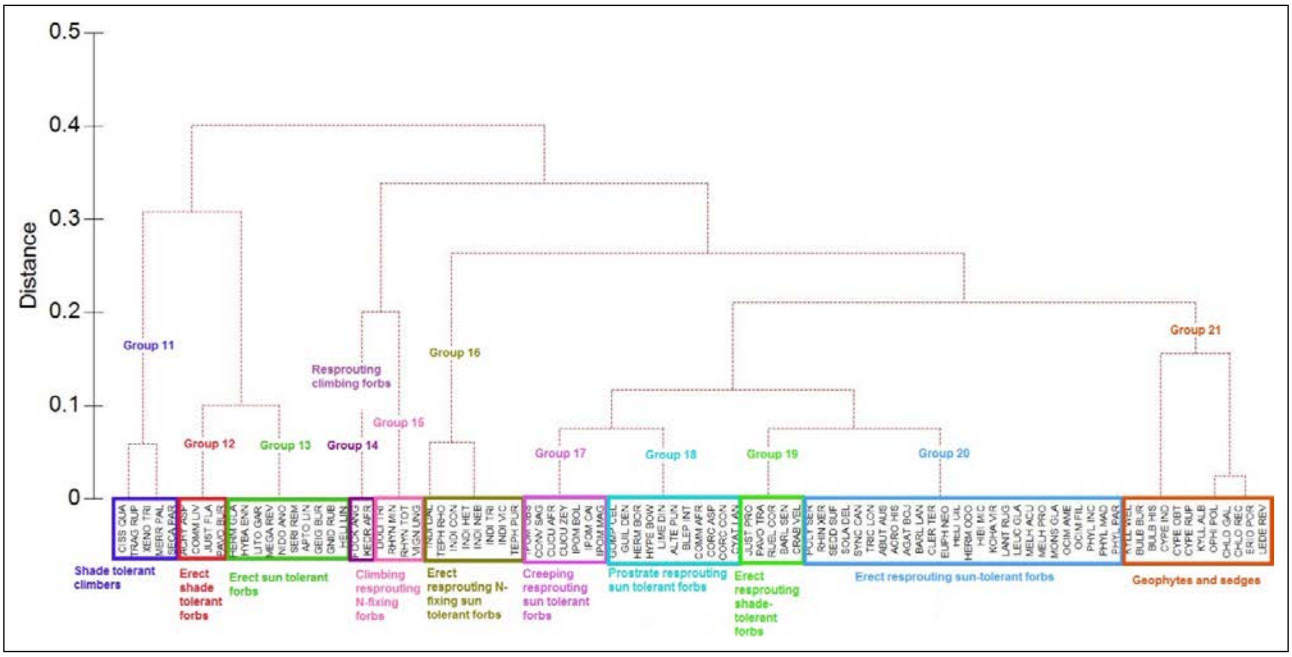

Figure S5. Unweighted Pair Group Method with Arithmetic Mean (UPGMA) based on Gower distance measure indicating perennial forb plant functional types (PFTs).

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A baseline assessment of the photosynthetic potential of *Welwitschia mirabilis* using the JIP-test for monitoring and conservation purposes

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Background: *Welwitschia mirabilis* is highly specialised to survive the harsh climate of the Namib Desert. Changes in land use, such as the expansion of mining activities, may endanger their survival.

Objectives: The purpose of this study was to understand the photosynthetic potential of *W. mirabilis* plants to provide a baseline for future long-term monitoring, and for future comparison to determine plant health status after the onset of mining operations.

Methods: The study was conducted in a population of *W. mirabilis* on the Welwitschia Plains. Chlorophyll a fluorescence data were used to measure plant photochemical potential and analysed using the JIP-test.

Results: Significant differences in the photosynthetic potential was observed for *W. mirabilis* plants located in different catchments. The partial parameters of the PI_{ABS} values were also significantly lower, which indicated that all aspects of photosynthesis were influenced.

Conclusion: PI_{ABS} values can serve as a baseline for future long-term monitoring studies to detect any changes in the health status of *W. mirabilis* that might result from land use change.

Keywords: chlorophyll a fluorescence, JIP-test, photosynthesis, PI_{ABS}, *Welwitschia mirabilis*, Welwitschia Plains

Introduction

Welwitschia mirabilis Hook.f. (Welwitschiaceae) is undoubtedly a desert oddity and, unlike most desert plants, has relatively large leaves. Its sheer size in comparison with other desert xerophytes emphasises its uniqueness (Veste 2008), together with its anatomy, cytology and habitat in which it is found (Schulze et al. 1976). *W. mirabilis* also has an unusual metabolic pathway; even though it displays a C3 photosynthetic pathway, it also exhibits CAM characteristics (Cooper-Driver 1994; Henschel & Seely 2000; von Willert et al. 2005).

Though more than one population of *W. mirabilis* exists within the Namib Desert, the Welwitschia Plains have the most plants and these are also the best-studied specimens (World Heritage Convention 2002). This area lies within the Namib-Naukluft Park and is the most accessible location for tourists to see these remnants from the Jurassic period (Cooper-Driver 1994). *W. mirabilis* plants form the dominant perennial vegetation in the area and provide shelter for numerous desert creatures such as arachnids, lizards and birds, and sustenance for oryx and zebra.

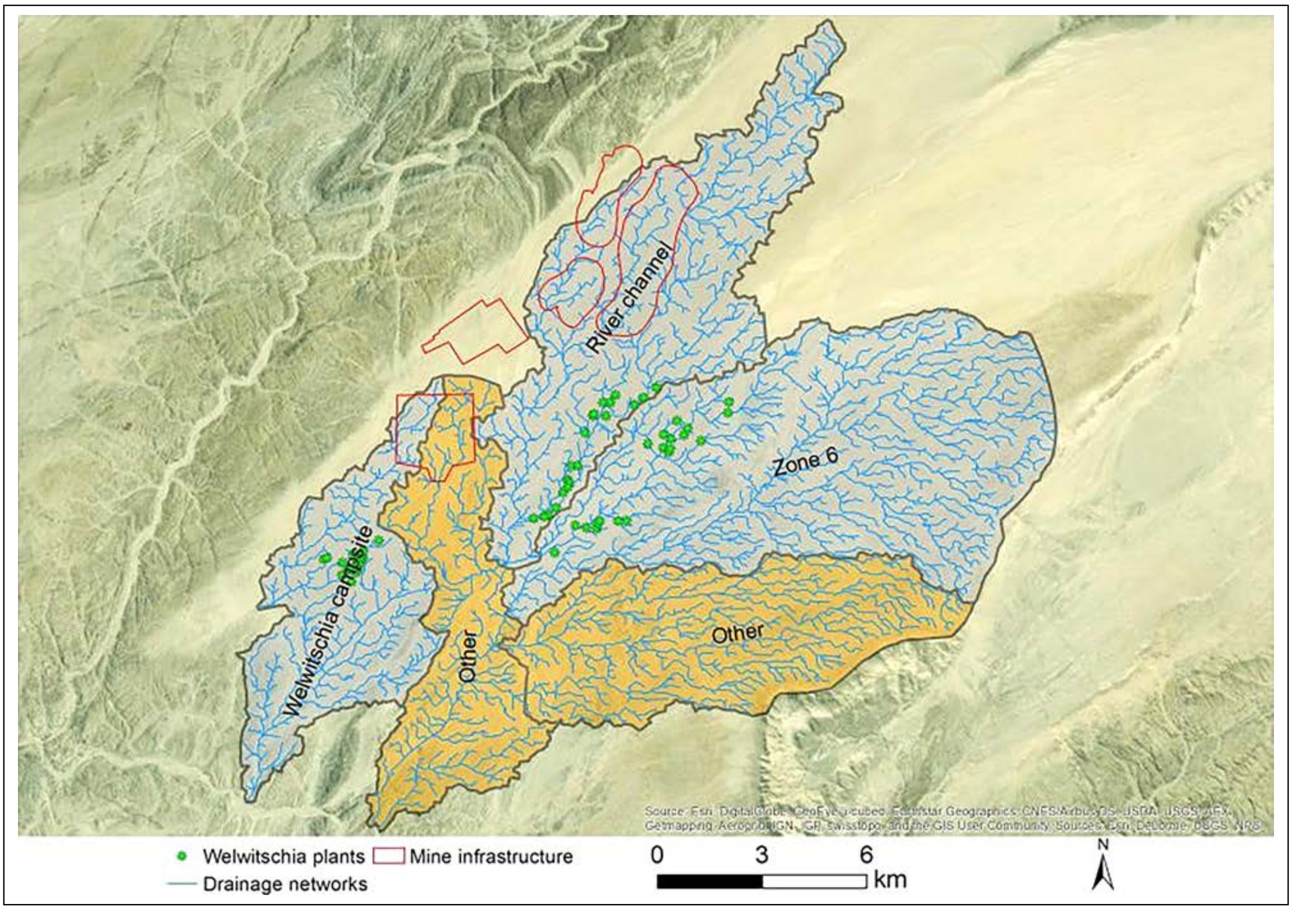

Figure 1. Outline of the three catchments (Campsite, Zone 6 and River Channel) showing their boundaries and surface drainage networks on the Welwitschia Plains. The two catchments indicated as 'other' were not included in the study. The mine infrastructure includes (from bottom to the top) the tailings dam, office, two pits and waste rock dump (long polygon on right). The selected welwitschia plants are indicated by green dots.

Mining in Namibia contributes substantially to its economy (Humavindu 2013), and uranium is currently being mined close to the Welwitschia Plains. This change in land use may pose a threat to the health and integrity of the surrounding desert ecosystem and, therefore, to the protection of *W. mirabilis* plants. The development of a management and monitoring plan to ensure the future of these iconic plants would be imperative, since *W. mirabilis* is a protected species under the Namibian Forest Act, No. 12 of 2001 and is also listed in Appendix II of the Convention on International Trade in Endangered Species (CITES).

Considering the species' protection status, a non-destructive and cost-effective method is required for monitoring. Chlorophyll *a* fluorescence-based techniques to assess plant health status, such as the JIP-test, is non-intrusive and widely employed to monitor stress (Busotti et al. 2010). Plants emit a fluorescence signal at a wavelength higher than 690 nm after exposure to actinic light. The JIP-test is then used to analyse the polyphasic rise of the chlorophyll fluorescence signal to gather valuable information about the plant's photosynthetic system (Strasser et al. 2004). Changes in the chemical and physical environment will lead to changes in the shape of the fluorescence transient and, therefore, it can be used to investigate the photosynthetic potential of plants. This study's objective was to understand the photosynthetic potential of *W. mirabilis* plants on the Welwitschia Plains to provide a baseline for future long-term monitoring of the plant health status for conservation purposes after the onset of mining operations.

Materials and method

The Welwitschia Plains are located approximately 60 km east of Swakopmund in the central Namib Desert, enclaved between the Swakop and Khan rivers (World Heritage Convention 2002). This area is characterised by rocky outcrops, inselbergs, rocky valleys, drainage networks and plains.

Rainfall patterns in the central Namib Desert are sporadic with an increase from the coast (~10 mm) eastwards (~60 mm at 100 km inland) (Shanyengana et al. 2002). Fog and dew are the primary water sources for many plants in the central Namib (Henschel & Seely

Table 1: Selected individual welwitschia plants measured at each catchment of the Welwitschia Plains with their corresponding GPS coordinates and gender

Catchment site	Plant number	Plant identity	Plant gender	GPS coordinates	
				Latitude	Longitude
Campsite	1	27424	Female	22°38′23.62″S	14°59′59.12″E
	2	30006	Male	22°38′33.67″S	14°59′43.71″E
	3	29115	Male	22°38′39.75″S	14°59′43.18″E
	4	29281	Female	22°38′40.66″S	14°59′41.26″E
	5	28322	Female	22°38′44.27″S	14°59′40.03″E
	6	29640	Female	22°38′42.84″S	14°59′38.17″E
	7	29602	Male	22°38′44.72″S	14°59′39.08″E
	8	29588	Female	22°38′44.98″S	14°59′37.37″E
	9	28831	Male	22°38′48.24″S	14°59′36.07″E
	10	28460	Female	22°38′50.68″S	14°59′38.17″E
	11	28444	Female	22°38′53.60″S	14°59′36.14″E
	12	28987	Male	22°38′50.58″S	14°59′30.53″E
River Channel	1	01169	Male	22°38′03.17″S	15°02′34.36″E
	2	07047	Male	22°38′01.28″S	15°02′44.98″E
	3	07024	Female	22°38′00.11″S	15°02′49.39″E
	4	06994	Male	22°37′53.05″S	15°02′56.40″E
	5	01982	Female	22°37′38.97″S	15°03′03.50″E
	6	02023	Female	22°37′33.63″S	15°03′08.47″E
	7	02051	Female	22°37′29.50″S	15°03′09.31″E
	8	02089	Female	22°37′27.32″S	15°03′08.16″E
	9	03551	Female	22°37′14.18″S	15°03′12.08″E
	10	02167	Female	22°37′13.89″S	15°03′18.45″E
	11	02463	Male	22°36′43.48″S	15°03′25.76″E
	12	03255	Male	22°36′27.54″S	15°03′33.28″E
Zone 6	1	10424	Male	22°38′09.63″S	15°03′16.20″E
	2	49611	Male	22°38′11.68″S	15°03′27.44″E
	3	49600	Male	22°38′12.45″S	15°03′37.36″E
	4	49669	Female	22°38′08.29″S	15°03′37.71″E
	5	49000	Male	22°38′05.56″S	15°03′40.61″E
	6	09014	Female	22°36′57.53″S	15°04′44.02″E
	7	05872	Male	22°36′44.91″S	15°04′44.51″E
	8	09096	Male	22°36′49.07″S	15°04′51.90″E
	9	09933	Male	22°36′39.24″S	15°05′08.74″E
	10	09891	Female	22°36′45.39″S	15°05′05.24″E
	11	10002	Female	22°36′58.27″S	15°04′51.45″E
	12	11011	Female	22°37′01.49″S	15°04′49.38″E

2000). Unlike rainfall, fog events and amount decrease with the distance from the coast, with 60–200 days of fog events recorded at Gobabeb (Henschel & Seely 2000; Shanyengana et al. 2002).

The study area was subdivided into three catchments areas due to observed differences in geological formations and topography, namely Campsite, River Channel and Zone 6 (Figure 1). Within each of these catchments, 12 individual plants were randomly selected for monitoring using ArcGIS 10.2 software (Supplementary Table 1) and were located in the field with their respective GPS coordinates.

Chlorophyll *a* fluorescence measurements of *W. mirabilis* plants were taken during winter (July) with a Handy Pea (Plant Efficiency Analyzer) fluorometer during the night. Measurements were taken one hour after sunset and continued to approximately midnight. Such dark adaption was done to ensure that all reaction centres were open. Ten fluorescence measurements were taken at different spots on each plant within the first 10 cm from the leaf base. During the time of the measurements, the night temperature was around 18°C. The Handy Pea was calibrated to produce pulses of light with an intensity of 3 445 μmol mol^{-1} and a gain of 1. These light pulses each had a duration of 1 second at a wavelength of 650 nm.

The chlorophyll fluorescence induction curve has specific inflection points named O, K, J, I and P, plotted on a logarithmic time scale (OJIP transient). Typically, stress will influence the shape of the OJIP transients by causing a shift in the induction curve. Assessing shifts in the induction curve provides information regarding the photosynthetic potential of the plant and, ultimately, plant health. The OJIP transient section between steps J and P is known as the thermal phase (or the multiple turn-over phase). This phase represents the reduction of the electron transport chain. The step between J and I is associated with the reduction of the PQ-pool and the I to P step with electron flow through photosystem I (Stirbet & Govindjee 2011).

The performance index (PI_{ABS}) is a widely used JIP-test parameter that provides quantitative information about the physiological state of plants and vitality. PI_{ABS} provides information about the potential for energy conservation from light absorption to the reduction of intersystem electron acceptors (Strasser et al. 2004). It is a function of its three partial parameters: the density of active reaction centres per chlorophyll ($\gamma_{RC}/(1-\gamma_{RC})$), the efficiency of electron movement by trapped excitation into electron transport chain ($\varphi_{PO}/(1-\varphi_{PO})$) and the probability that the reaction centres will trap an absorbed photon ($\psi_{Eo}/(1-\psi_{Eo})$) (Strasser et al. 2000). If a stress condition influences any of these partial parameters, the stress will influence the PI_{ABS} values and reflect the current state of photosynthetic performance (Strasser et al. 2004).

The fluorescence data captured with the Handy Pea was analysed with PEA Plus 1.140 software. The River Channel was selected as the reference site as the plants represented at this site were visually larger and appeared healthier compared to the other two sites. The translation of the fluorescence data to biophysical parameters was done according to Strasser et al. (2004). Data were subjected to the Shapiro-Wilk test and if data conformed to the assumptions of normality, a one-way ANOVA was run for each parameter in Statistica v13, Dell Inc. (2016).

Results

Typical chlorophyll *a* fluorescence induction curves of dark-adapted leaves of *W. mirabilis* plants were plotted for the Campsite, River Channel and Zone 6 catchments (Figure 2). The time frame between steps O and J (also referred to as the single turn-over phase or the photochemical phase) provides information about the antenna size and the connectivity between photosystem II reaction centres (Strasser et al. 2004). When the induction curves from the different catchments were compared to one another during this time frame, there were no apparent shifts in the induction curve from any of the catchments (Figure 2). A shift in the shape of the Campsite induction curve was observed between steps I and P. The rise in the fluorescence transient, especially after the I-step, was the lowest at Campsite. This would imply that the electron flow between photosystem II and photosystem I was less efficient (Figure 2).

W. mirabilis plants located at Campsite had significantly lower PI_{ABS} ($P < 0.05$) values when compared to the other catchments (Figure 3). The lower PI_{ABS} values of Campsite suggests that these *W. mirabilis* plants are in a less optimal condition. By normalising the JIP parameters of Campsite and Zone 6 to River Channel (references site), differences among the catchments were emphasised. From the spider plot it was clear that all of the parameters that comprise the PI_{ABS} values for Campsite were all lower than those of River Channel and Zone 6 (Figure 4). The density of active reaction centres ($\gamma_{RC}/(1- \gamma_{RC})$), the potential to create a charge separation ($\varphi_{PO}/(1- \varphi_{PO})$) and the potential to transport electrons between PSII and PSI ($\psi_{Eo}/(1-\psi_{Eo})$) were all lower at Campsite (Figure 4).

The total performance index, PI_{total}, is the product of the PI_{ABS} and the probability that an electron can move from a reduced intersystem electron acceptor to the PSI end-electron acceptors (Tsimilli-Michael & Strasser 2008). The PI_{total} index is, therefore, very closely related to the plants' overall growth and health. The PI_{total} values of the welwitschia plants growing at Campsite were also significantly lower ($P < 0.05$). The only difference between the PI_{total} and the PI_{abs} is that for calculating the PI_{total} index, the reduction of the end electron acceptors

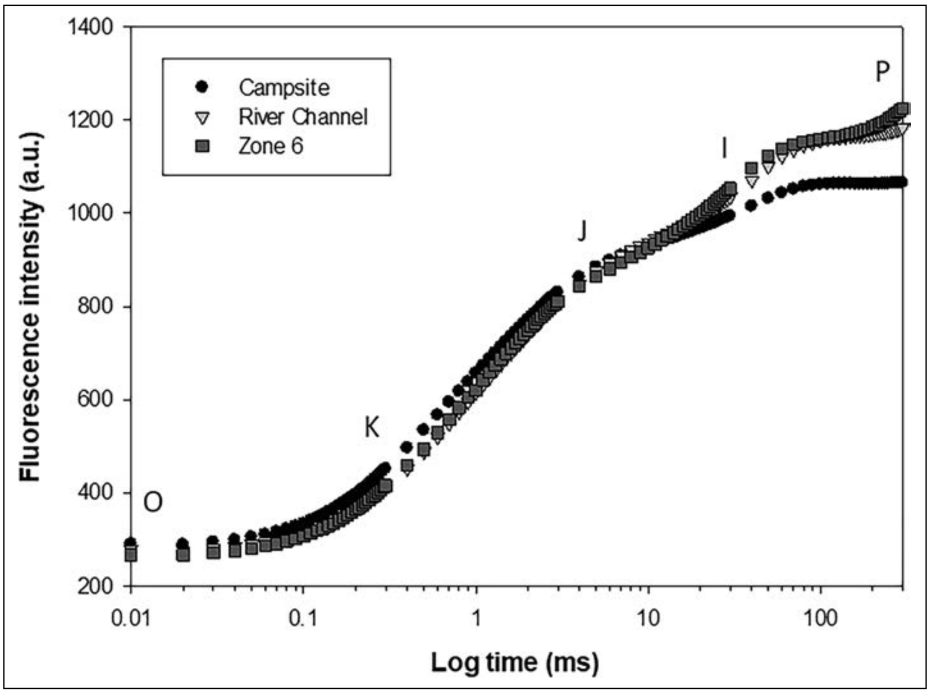

Figure 2. OJIP transient of dark-adapted welwitschia plants located in the catchments of the Welwitschia Plains, taken during July 2015.

($\delta_{Ro}/(1-\delta_{Ro})$) is included. Overall the spider plot (Figure 4) clearly shows that the photosynthetic potential of the *W. mirabilis* plants at Campsite was less efficient compared to the other two catchments.

Discussion

Monitoring the health status of *W. mirabilis* plants is critical for early detection of the impact of land-use change. Chlorophyll *a* fluorescence measurements, which were taken before the onset of mining activitiesm, can now serve as a baseline for future monitoring (Kalaji et al. 2016). The vitality statuses of plants before mining activities is indicated by differences in the photosynthetic potential between *W. mirabilis* plants located within different catchment areas in the same locality. The maximum photosynthetic quantum yield of *W. mirabilis* plants located at Campsite was lower than River Channel and Zone 6, indicating a less optimal health condition when compared to the latter two.

The Campsite catchment has a higher elevation than the other catchments resulting in lower water accumulation, as water accumulates along the flow paths, which is influenced by the topography (Fan et al. 2020). This lower water accumulation at Campsite will lower

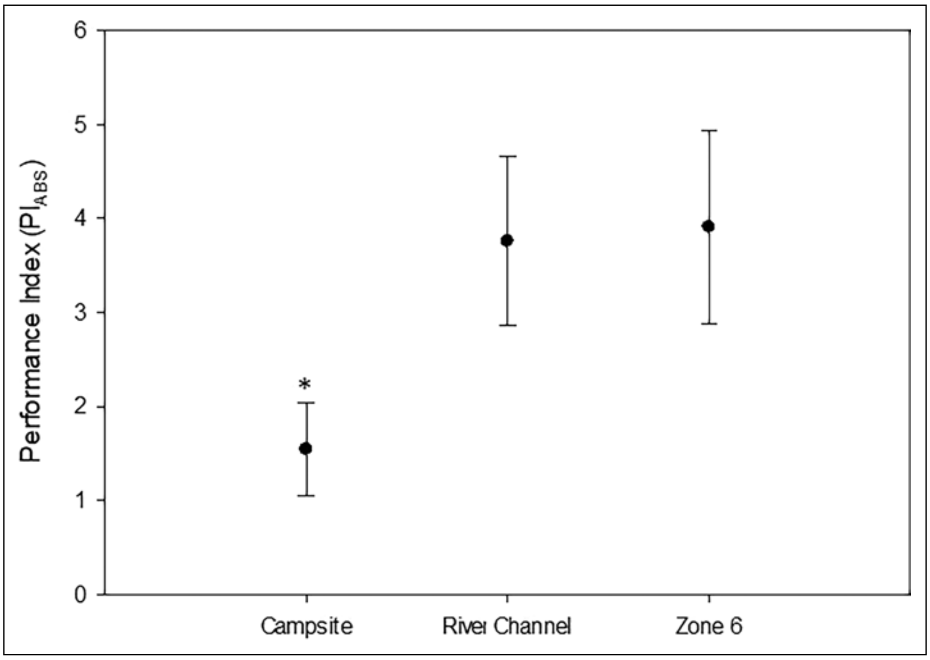

Figure 3. The performance index values (PI_{ABS}) of the welwitschias located at the Campsite, River Channel and Zone 6 catchments. The asterisk (*) denote significant ($P < 0.05$) differences from the other catchments.

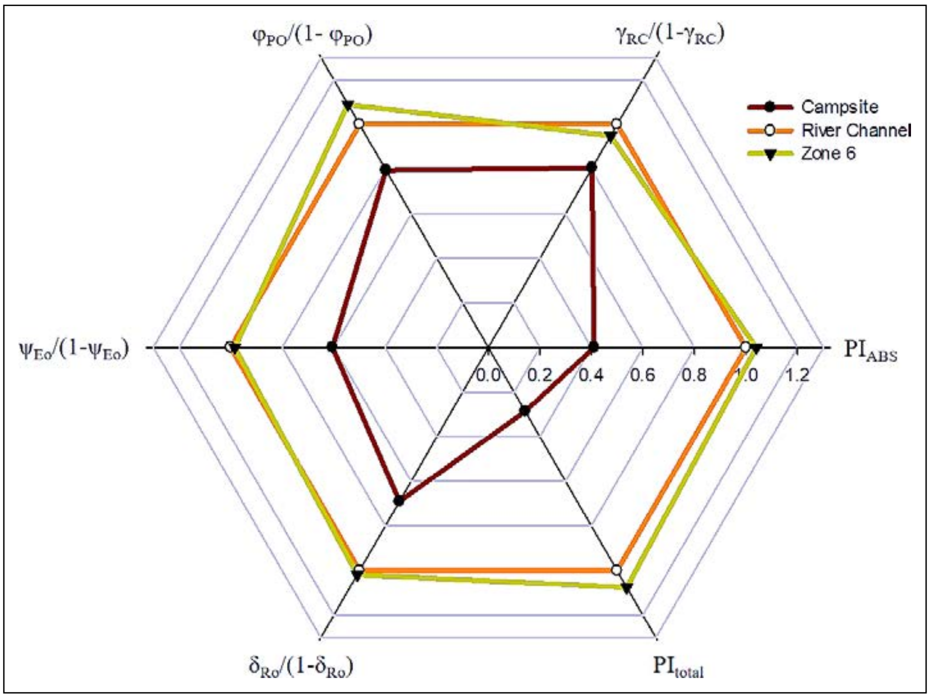

Figure 4. Spider diagram indicating the difference in the partial parameters between the different sites. The River Channel catchment was used as a reference with which the Campsite and Zone 6 catchments were compared.

the photosynthetic potential of the *W. mirabilis* plants. Topographic features such as elevation and slope may also change vegetation exposure to wind and solar radiation, contributing to a decrease in the photosynthetic potential (Mikita & Klimánek 2010). Because this study was conducted during winter, episodic rainfall did not influence the measurements. Incoming fog from the Atlantic Ocean might influence the photosynthetic potential of plants and has to be acknowledged, but the selected welwitschia plants for this study were chosen from outside the reach of the incoming fog.

For all practical reasons, the PI_{total} performance index or any partial parameters could have been used (Kalaji et al. 2016). To optimise the value of the JIP-test, annual readings should be taken on the same plants and any changes in the JIP parameters should be noted. It is recommended that several measurements be taken throughout the year. The data from this study represent the environmental conditions during the winter and if this same investigation was carried out during the summer, different PI_{ABS} values would be obtained, but the trend should remain the same (Janssen & Hasselt 1994).

Considering the planned change in anthropogenic activities, together with natural stressors on the fringes of the Welwitschia Plains, it is imperative to detect changes in the health status before the onset of visible stress symptoms. This early detection of plant stress will prompt for management actions to prevent populations from being adversely affected (Chaerle & Van Der Straeten 2000). Therefore, the chlorophyll fluorescence parameters analysis can be a very informative tool in ecological surveys (Kalaji et al. 2016) by providing explanations on the physiological behaviour of *W. mirabilis* plants in response to its changing environment. We suggest that long-term monitoring studies integrating potential drivers and responses be conducted to understand the plant health of *W. mirabilis* across the landscape. This study has established a baseline that can be used to develop a protocol to monitor the plant physiological status and the possible management strategies for mines and other developments that may have adverse impacts on the *W. mirabilis* population. Besides that, the findings may also aid restoration and rehabilitation measures such as transplantation and re-introduction of this species by understanding its current functional health status across the landscape over time.

Conclusion

Chlorophyll a fluorescence measuring techniques have high potential to investigate plant health *in situ* in long-term monitoring. Our study was a preliminary one, conducted over only a short period. Considering the longevity of welwitschia plants and the urgent need to develop a thorough understanding of how the species reacts to different stressors created by land-use change, longer-term studies should be conducted to understand the *in situ* spatial and temporal patterns of the species' health. With increasing mining activities on the fringes of the Welwitschia Plains and the potential threat that these anthropogenic activities pose to the welwitschia population, continued monitoring is vital.

Acknowledgments

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Authors’ contributions

JMB planned and coordinated the study, collected field data, conducted data analyses and wrote the manuscript. HC collected field data, conducted data analyses and contributed to the writing of the manuscript. TS collected field data and contributed to the analysis & interpretation of the data.

Disclaimer

The views expressed in the submitted article are our own and not an official position of the institution or funder.

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Drought tolerant forb flora of a semi-arid protected savanna in the Lowveld of South Africa

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Background: Increased frequency and intensity of droughts related to climate change are predicted to induce pressure on herbaceous communities. Considering that forbs contribute significantly to savanna ecosystem resilience, we investigated forb communities of a protected semi-arid savanna during an extensive drought.

Objective: We identified drought-tolerant species with their related functional traits.

Results: Drought-tolerant forb flora comprised of several plant families and species with overlapping traits, of which the ability to resprout was related to perennials, whereas succulence and prostrate growth form were typical annual forb dominance traits.

Conclusion: Results highlight the functional importance of forbs and their resilience to drought events in protected areas.

Keywords: resprouting; herbaceous communities; functional traits; resilience; climate change.

Introduction

Predicted increasing drought intensity and frequency, combined with higher average temperatures due to global climate change, are threatening biodiversity, and therefore the stability, functioning and sustainability of terrestrial ecosystems (Barros et al. 2018). Drought is a common phenomenon in semi-arid rangelands (Vetter 2009) and has been shown to cause rapid and lasting effects on vegetation dynamics and ultimately ecosystem function and services (Barros et al. 2018; Ploughe et al. 2019).

Depending on intensity, droughts can cause shifts in plant species assemblages, leading to the establishment of different plant communities (Junk et al. 2018). In herbaceous layers of semi-arid savannas, these communities are composed mainly of annual grasses and both annual and perennial forbs (O'Connor 1998; Buitenwerf et al. 2011). In the savanna context, the term 'forb' is used to classify anything other than trees, shrubs and grasses, which has led to a poor functional definition of this life form. For the purpose of this study, we will define forbs as non-graminoid vascular plants with limited woody tissue and with perennating buds at or below soil surface. Drought episodes tend to favour forbs, since they possess a variety of drought-tolerant traits such as underground storage organs (Siebert et al. 2019) associated with persistent bud banks and viable seed banks (Siebert & Dreber 2019). Despite being associated with savanna land degradation and therefore perceived as being an undesirable functional group by land managers (Fynn & O'Connor 2000; Tessema et al. 2011), forbs are important through providing ecosystem functions (i.e. forage stability) during stressed conditions, and functional redundancy to absorb disturbances such as sustained grazing and droughts (Van Coller et al. 2018).

Forbs are an important source of nutritious forage and may constitute an important part of ungulate diets at certain times of the year (Du Toit 2003; Van Der Merwe & Marshal 2012). Moreover, forbs contribute significantly to the biodiversity of savanna and grassland systems (Buitenwerf et al. 2011; Siebert & Scogings 2015), which are functionally diverse, suggesting a stronger resilience to different environmental conditions (Turner & Knapp 1996; Van Coller et al. 2018). Forb ecology research in dry African savannas generally report on forb responses at the level of functional group rather than species level. Furthermore, variations in forb functional traits defining plant strategies for regeneration and survival in adaptation to climate extremes such as droughts, remain understudied (Siebert & Dreber 2019).

Below-average rainfall in the Central Lowveld of South Africa was recorded for two consecutive years (2015 and 2016) (Swemmer et al. 2018). Using data collected during this time, we sought to identify specific drought tolerant forb species and their respective functional traits in a semi-arid African savanna. In doing so, we aimed to enhance knowledge of the attributes that allow these forb species to persist during droughts and potential functions that they fulfil under such environmental conditions.

Materials and Methods

Forb communities were studied in the semi-arid savanna of the greater Kruger National Park (KNP). Protected areas are not exempt from natural disasters, such as drought. They therefore provide valuable natural experimental settings where spatial heterogeneity and ecological responses function under natural drivers (Pickett et al. 2003). These areas host a variety of indigenous wildlife including mixed feeders (e.g. elephants [*Loxodonta africana* (Blumenbach, 1797)]; impala [*Aepyceros melampus* (Lichtenstein, 1812)]), browsers (e.g. greater kudu [*Tragelaphus strepsiceros* (Pallas, 1766)]; bushbuck [*Tragelaphus sylvaticus* (Sparrman, 1780)]), and grazers (e.g. blue wildebeest [*Connochaetes taurinus* (Burchell, 1823)]; plains zebra [*Equus quagga* (Boddaert, 1785)], amongst others (Van der Waal et al. 2011; Scogings et al. 2012).

Field surveys were undertaken at two sites of similar geology (i.e. granite and gneiss), but different soil nutrient statuses (i.e. nutrient-rich sodic soil versus nutrient-poor sandy soil). Floristic and functional trait data were collected from 48 plots of 1 m^2 (18 plots within the nutrient-rich site and 30 plots within the nutrient-poor site) during the usual rainy season (November–March) of the extensive drought of 2015/2016. In the KNP (i.e. nutrient-rich site), total annual rainfall was 200 mm below the mean annual rainfall for the area (Van Coller et al. 2018), while at the nutrient-poor site in Timbavati Private Nature Reserve (TPNR) it was ~330 mm below the long-term average (Kaschula et al. 2005). Within each plot, forbs were identified up to species level and all individuals counted. Frequency per species was calculated with respect to all recorded species in each respective site. Frequency is considered a stable variable for the abundance of an individual species (O'Connor 2015). Frequency measures (%) were used to identify forb species most commonly observed in the study sites. Only forb species with a frequency ≥ 1 are discussed. Functional traits were assigned to forb species (Cornelissen et al. 2003; Germishuizen & Meyer 2003) based on the potential contribution to the functioning of semi-arid protected areas (i.e. palatability, life history and nitrogen-fixing ability), as well as the ability to tolerate conditions related to drought and herbivory (growth form, life history, resprouting capacity and succulence).

Results and Discussion

Herbaceous productivity is strongly affected by rainfall, and generally reveals marked deterioration in response to drought conditions (Figure 1) (Fynn & O'Connor 2000; O'Connor 2015). Despite this, frequency measures revealed a total of 31 forb species among the two study sites. A mean number of six and four forb species was recorded per plot (1 m^2) in the nutrient-rich and nutrient-poor sites respectively. The number of forb species per plot recorded in the nutrient-rich site ranged from one to 17, while a lower range (0–7) of forb species were recorded for plots in the nutrient-poor site.

Plant families that comprised most of the frequent taxa during the drought included Acanthaceae and

Figure 1. Sparsely vegetated sampling sites within the KNP (A) and TPNR (B) during the drought.

Amaranthaceae in the nutrient-rich site, and Fabaceae and Boraginaceae in the nutrient-poor site (Table 1). Prevalence of the Fabaceae is in accordance with Wagner et al. (2016) who reported that nitrogen-fixing herbaceous legumes from the Fabaceae may increase in abundance after disturbances in dry savanna rangelands, and also in disturbed grasslands (Muller et al. 2021). Nitrogen-fixing ability is a trait generally associated with ecosystems with low nutrient availability (Cornelissen et al. 2003), explaining the high frequency of *Chamaecrista mimosoides* (L.) Greene in the nutrient-poor site (Table 1). Over 50% of the most frequent forbs were annuals (Table 1). Annual forbs have been reported to form a major component of soil seed banks, especially under heavy grazing (O'Connor 1991; Tessema et al. 2016), potentially enabling them to respond and establish rapidly when conditions become favourable (e.g. smaller rainfall events interrupting extensive droughts). The occurrence of bare soil caused by herbivores and drought is known to facilitate the colonisation of prostrate forb species (Burkepile et al. 2016). *Blepharis integrifolia* (L.f.) E.Mey. ex Schinz, a palatable, perennial and low-growing forb is known to form patches of continuous groundcover or 'browsing lawns' in heavily utilised sodic bottomlands (Siebert & Scogings 2015), whilst the prostrate-growing annual *Gisekia africana* (Lour.) Kuntze revealed the highest frequency in the nutrient-poor site (Table 1). Persistence of these species is therefore likely attributed to the positioning of perennating tissue at or close to the soil surface, since fewer species could have buds far above the soil surface during harsher climatic conditions such as drought (Cornelissen et al. 2003). Moreover, erect growing plant species with their perennating buds situated above the soil surface are especially susceptible to trampling, heavy grazing and exposure to extreme heat conditions, whereas prostrate-growing species are avoidant by retaining buds and leaf material close to the soil surface (Cornelissen et al. 2003). A prostrate growth form in forbs could therefore be considered an important resistance trait against drought and grazing in the protected Lowveld savannas of South Africa.

The presence of annual forb species with a pioneer character in seed banks (Tessema et al. 2016) allows for their initial colonisation of bare soil (Siebert & Dreber 2019). Therefore, some of the most frequently observed forb species during the drought (i.e. *Portulaca kermesina* N.E.Br. and *P. hereroensis* Schinz in the nutrient-rich site, and *G. africana* in the nutrient-poor site) were annuals (Table 1). Moreover, these species exhibited traits generally associated with grazing- and drought-tolerance (i.e. prostrate growth form and succulence) (Cornelissen et al. 2003). Although little is known about succulence as a drought-tolerant trait in forbs, the ability of these species to retain water in their leaves and stems during dry conditions, together with a prostrate growth form to avoid and tolerate herbivory, possibly favoured their survival when subjected to herbivore utilisation in dry, hot conditions. Annual forbs exhibiting this combination of traits therefore make up an important component of the forb flora of semi-arid protected areas, especially during a drought.

The majority of drought-tolerant perennial forbs in this study had the ability to resprout, either through buds located at or near the soil surface, or belowground. Such a disturbance-tolerant trait is well-known for trees and shrubs, but our understanding of regeneration from buds in forbs is unknown and requires further investigation (Siebert & Dreber 2019).

Over half of the frequent forb species recorded during the drought were palatable (Table 1). This reinforces the functional importance of the forb component through their ability to provide important ecosystem functions, such as forage stability during stressed conditions, and functional redundancy enabling them to absorb disturbances such as sustained grazing and drought (Van Coller et al. 2018).

Conclusion

Despite anticipated deterioration of the herbaceous layer during droughts, forbs have the ability to withstand such disturbances through species-specific adaptions. Numerous forb species were able to persist amidst the abnormal hot and dry conditions, while providing the ecosystem with important functions and services, such as forage stability. Plant strategies for survival and regeneration during drought conditions are species- and family specific, which may vary across ecosystem types. Furthermore, drought-adaptations were also specific for life history groups, as annuals displayed strategies to survive after emergence (e.g. succulence and prostrate growth form), whilst the majority of perennial forbs had the ability to resprout from a persistent bud bank. As protected areas aim to conserve biodiversity, provide forage security for wildlife and to maintain ecosystem resilience, this study demonstrates that forbs contribute to these at plant taxonomic and functional trait levels.

Authors' contributions

HvC (North-West University) collected vegetation data from the Nkuhlu exclosures at the Kruger National Park (KNP), analyzed and reported data and wrote the manuscript, whilst JK (North-West University) collected data from Timbavati Private Nature Reserve (TPNR). FS (North-West University) was the project leader, promoter and supervisor to HvC and JK respectively, and was responsible for project design, data collection, reporting and the writing of the manuscript.

Disclaimer

The authors declare that the work presented, and views expressed in this submitted article is their own and is

Table 1: Frequent forb species in the semi-arid savanna of the Greater KNP during a drought with a summary of relevant functional traits. Trait data were derived from field guides and various Floras

Species	Family	Life history	Growth form	Palatability§	Resprouting capacity	Nitrogen fixator	Succulence	Frequency
Nutrient-rich site (KNP)								
Blepharis integrifolia (L.f.) E.Mey. ex Schinz	Acanthaceae	Perennial	Prostrate	High	Aboveground	No	No	45.8
Portulaca kermesina N.E.Br.	Portulacaceae	Annual	Prostrate	High	–	No	Leaves and stems	5.8
Ruellia cordata Thunb.	Acanthaceae	Perennial	Erect leafy	High	Belowground	No	No	4.4
Phyllanthus incurvus Thunb.	Euphorbiaceae	Perennial	Erect leafy	Moderate	Aboveground	No	No	4.0
Bidens bipinnata L.*	Asteraceae	Annual	Erect leafy	Moderate	–	No	No	2.8
Waltheria indica L.*	Sterculiaceae	Perennial	Erect leafy	Low	Aboveground	No	No	2.6
Portulaca hereroensis Schinz	Portulacaceae	Annual	Prostrate	Low	–	No	Leaves and stems	2.5
Acalypha indica L.	Euphorbiaceae	Annual	Erect leafy	Moderate	–	No	No	2.1
Commelina benghalensis L.	Commelinaceae	Annual	Erect leafy	High	Above and belowground	No	No	2.1
Hibiscus micranthus L.f.	Malvaceae	Perennial	Erect leafy	High	Belowground	No	No	2.1
Kyphocarpa angustifolia (Moq.) Lopr.	Amaranthaceae	Annual	Erect leafy	High	–	No	No	2.1
Ocimum americanum L.	Lamiaceae	Perennial	Erect leafy	Low	Aboveground	No	No	2.1
Evolvulus alsinoides (L.) L.	Convolvulaceae	Annual	Erect leafy	Moderate	–	No	No	1.4
Gomphrena celosiodes Mart.*	Amaranthaceae	Perennial	Prostrate	Moderate	Aboveground	No	No	1.4
Justicia flava (Vahl) Vahl	Acanthaceae	Perennial	Erect leafy	Moderate	–	No	No	1.4
Achyranthes aspera L.*	Amaranthaceae	Perennial	Erect leafy	High	–	No	No	1.2
Indigofera filipes Benth. ex Harv.	Fabaceae	Annual	Erect leafy	Moderate	–	Yes	No	1.2
Nutrient-poor site (TPNR)								
Gisekia africana (Lour.) Kuntze	Gisekiaceae	Annual	Prostrate	Low	–	No	Leaves and stems	35.3
Chamaecrista mimosoides (L.) Greene	Fabaceae	Annual	Erect leafy	Moderate	–	Yes	No	11.2
Heliotropium strigosum Willd.	Boraginaceae	Annual	Erect leafy	Low	–	No	No	6.0
Commelina benghalensis L.	Commelinaceae	Annual	Erect leafy	High	Above and belowground	No	No	4.8
Leucas sexdentata Skan	Lamiaceae	Annual	Erect leafy	Low	–	No	No	4.4
Phyllanthus maderaspatensis L.	Euphorbiaceae	Perennial	Erect leafy	Moderate	Aboveground	No	No	4.1
Chamaecrista absus (L.)Irwin & Barneby	Fabaceae	Annual	Erect leafy	Low	–	Yes	No	2.3
Phyllanthus parvulus Sond.	Euphorbiaceae	Perennial	Erect leafy	Moderate	–	No	No	2.3
Schkuhria pinnata (Lam.) Cabrera*	Asteraceae	Annual	Erect leafy	Low	–	No	No	1.8
Sida ovata Forsk.	Malvaceae	Annual	Erect leafy	Low	Belowground	No	No	1.8
Bidens bipinnata L.*	Asteraceae	Annual	Erect leafy	Moderate	–	No	No	1.6
Heliotropium ovalifolium Forssk.	Boraginaceae	Annual	Erect leafy	Low	Belowground	No	No	1.6
Heliotropium ciliatum Kaplan	Boraginaceae	Perennial	Erect leafy	Low	Belowground	No	No	1.4
Tephrosia longipes Meisn.	Fabaceae	Annual	Erect leafy	Low	Aboveground	No	No	1.4

§ This categorical trait is based on an adapted version of Walker's Palatability Index (Siebert & Scogings 2015), to detect browsing signs from smaller ungulates. Species preference of larger herbivores (e.g. elephant) remains poorly known as they often uproot the entire plant. For the purpose of this trait data, a forb was considered palatable if it showed any signs of browsing, irrespective of the type of large herbivore; Alien species are indicated with asterisk (*).

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A floristic assessment of grassland diversity loss in South Africa

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Background: Land-use effects on grassland flora are difficult to predict due to poor understanding of species losses caused by transformation.

Objectives: To determine changes in species diversity and composition by comparing transformed with untransformed grassland.

Methods: Floristics of paired plots were sampled within 18 transformed sites (representing agricultural and urban land-uses) and neighbouring untransformed grassland.

Results: Endemic and threatened species were negatively affected by transformation, particularly species with belowground bud-banks and storage organs. Species composition, with clear shifts in dominant families, was changed by over 90% on average by transformation.

Conclusion: Land-use transformation lead to the loss of native species and increased alien invasive species.

Introduction

Land-use change threatens the persistence of many grassland ecosystems worldwide (Bond 2016). Grasslands are hyper-diverse ancient ecosystems, habitats and communities, supporting many endemic and threatened species (Carbutt, Henwood & Gilfedder 2017). Habitat transformation threatens the integrity of these systems through soil disturbance and the removal of plant biomass and species, and the effect is widely recognised and measurable (Herben, Chytrý & Klimešová 2016; Miller, Roxburgh & Shea 2011). The poor understanding of forb dynamics in grassland necessitates a closer look at floristic change and whether land-use change leads to species losses or gains in transformed grassland (Veldman et al. 2015).

In South Africa the Grassland Biome covers approximately one third of the land surface (Carbutt et al. 2011). The extent of grassland is defined on the basis of vegetation structure, as well as environmental factors including mean summer rainfall and minimum winter temperatures (Mucina & Rutherford 2006). The Grassland Biome is one of the most at-risk South African biomes, with 40–60% irreversibly modified, and less than 3% formally protected (Little, Hockey & Jansen 2015). The intactness of unprotected South African grasslands is threatened as there is an increase in the intensity of agriculture and afforestation (O'Connor & Kuyler 2009; Botha et al. 2017) and urban and industrial development activities (Siebert, Van Wyk & Bredenkamp 2001; O'Connor & Kuyler 2009). Changes in composition, structure and functioning of these grasslands influence the ability to deliver fresh water, soil formation, climate regulation and reduction of disaster risk (Egoh et al. 2011), and in addition, probable loss of biodiversity and grassland production (Everson & Everson 2016).

O'Connor and Kuyler (2009) have meticulously investigated the impact of land-use on the biodiversity integrity of moist grasslands in South Africa and highlighted the loss of useful plants from an ecosystem services perspective. Our study focusses on biodiversity intactness in that it specifically considers loss of native floristic diversity. It places special emphasis on the indigenous forb component that is fast moving up the research agenda (Siebert & Dreber 2019).

Materials and methods

Study area

Eighteen study sites were selected in four bioregions of the Grassland Biome, as well as a tropical bioregion of the Indian Ocean Coastal Belt Biome of South Africa (Figure 1). The chosen grasslands occurred at altitudes ranging between 30 and 3 100 m above sea level, with ten sites between 1 000 and 1 800 m. The mean annual temperature for the grassland sites ranged from 10 to 21°C, with an overall mean of 16.3°C (median 15.9°C). June to August are the coldest months with mean frost days per annum varying between 0 and 96, with a mean of 25 (median 28) across all study sites (Mucina & Rutherford 2006). All sites experience summer rainfall ranging from 600 to 1 000 mm per year and a mean of 761 mm (median 717 mm) across sites. Twelve sites receive less than 800 mm per annum.

Field surveys

Two dominant land transformation types in the Grassland Biome were included in this study, namely agriculture and urbanisation (Neke & Du Plessis 2004). Floristic data were gathered from 18 sites. At each site, sampling was conducted in four plots in untransformed grassland, each paired with a plot in an adjacent transformed land-use (i.e. eight plots per site), no more than 150–250 m apart. All 144 plots were surveyed in late spring or early to mid-summer. Each 100 m^2 plot was divided into 25 subplots of 4 m^2 each to record species occurrence and abundance. Species were identified in the field and photos were taken for later confirmation. Floristic data from the subplots were combined to compile a total inventory for each 100 m^2 plot.

Plant species nomenclature and classification follow Ranwashe (2019). Naturalised and invasive categories are according to Department of Environmental Affairs (2016). Life and growth forms of plant species were

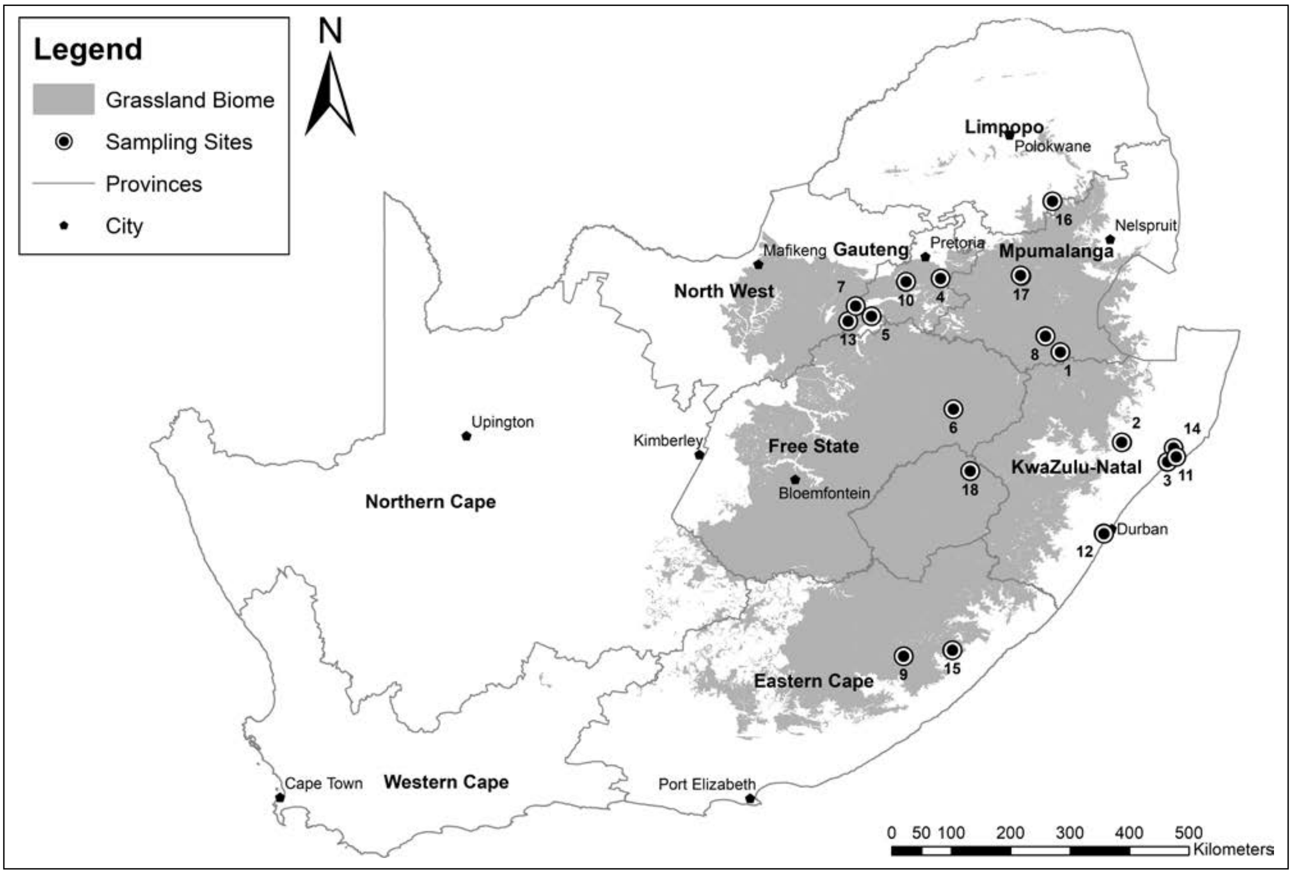

Figure 1. Location of the 18 study sites in the Grassland Biome of South Africa. Land-use transformation at localities: Agriculture, afforestation: 1, 2, 3; field margins: 4, 5, 6; abandoned fields: 7, 8, 9; urban, green space: 10, 11, 12; peri-urban: 13, 14, 15; mine rehabilitation: 16, 17, 18.

obtained from Germishuizen and Meyer (2003). Categories of threat were obtained from the Red Data List of South African Plants (South African National Biodiversity Institute 2017).

Species abundance (N) was calculated as the total number of individuals and species richness (S) as the total number of species within each 100 m^2 plot. The Shannon–Wiener (H′) and Pielou (J′) indices were applied to plot data to calculate alpha diversity and evenness respectively. All above values were calculated using Primer (2007).

Data analysis

Non-Metric Multi-Dimensional Scaling (NMDS) analysis in Primer (2007) was used to explore changes in species composition between transformed and untransformed grasslands. Permutational Multivariate Analysis of Variance (PERMANOVA) was performed using species abundance data. Analyses were conducted with 999 permutations using Bray–Curtis similarity and Type III sums of squares after a square root transformation of species data to reduce the influence of common species. To account for location variability in the paired, nested sampling design, plots were treated as a random variable nested within a transformation type (i.e. urban or agricultural), which were treated as the fixed factor. Pair-wise test results indicated the strength of the difference between transformed and untransformed plots.

Similarity Percentage Analysis (SIMPER) was applied to determine which forb and grass species contributed the most to differences between transformed and untransformed grasslands. Simple paired t-tests were applied to test for significant differences between untransformed and transformed plots for selected diversity measures. Percentage decrease in richness and abundance of species per growth/life form, threat status, endemism and for alien taxa was calculated from the statistical means.

Results

Floristics

Overall, 1 146 plant species were recorded, of which 144 were non-native. The untransformed grassland contained 962 species, which included 35 naturalised and 15 invasive taxa (5%), 175 South African endemics (18%) and 20 threatened species (2%). The transformed grasslands had 582 species, including 92 naturalised and 46 invasive taxa (24%), 47 South African endemics (8%) and six threatened species (1%).

The most prominent families in the localities were the Asteraceae, Poaceae, Fabaceae and Cyperaceae in order of most species diverse (Table 1), whereas the Poaceae were most abundant (Table 2). It is evident that transformation is less favourable to the Asteraceae and Fabaceae, and more beneficial to the Cyperaceae and especially the Poaceae.

Habitat transformation affects the number of species present per family. The geophytic Hyacinthaceae and Iridaceae showed the largest species losses (18 and 19 species respectively) when grassland is transformed and

Table 1. Top ten families of untransformed and transformed grasslands based on the proportion of each family's contribution to the total species pools of 962 and 582 respectively. Superscripts indicate up or down movement in ranking in transformed grassland

Family	Proportion of all species (%)		Shift in ranking
	Untransformed	Transformed	
Asteraceae	20,4	19,6	1 / 1
Poaceae	12,9	17,1	2 / 2
Fabaceae	10,2	10,1	3 / 3
Cyperaceae	3,6	3,1	4 / 4
Apocynaceae	3,2	1,7	5 / 10 $^{\vee 5}$
Malvaceae	2,5	2,9	6 / 5 $^{\wedge 1}$
Scrophulariaceae	2,4	1,5	7 / 11 $^{\vee 4}$
Iridaceae	2,3	0,7	8 / 23 $^{\vee 15}$
Hyacinthaceae	2,2	0,5	9 / 31 $^{\vee 22}$
Lamiaceae	2,1	1,9	10 / 7 $^{\wedge 3}$
Amaranthaceae	0,5	2,4	30 / 6 $^{\wedge 24}$
Solanaceae	0,6	1,8	36 / 9 $^{\wedge 27}$

Table 2. Top ten families of untransformed and transformed grasslands based on the proportion of each family's contribution to total recorded individuals of 20 640 and 12 042 respectively. Superscripts indicate up or down movement in ranking in transformed grassland

Family	Proportion of all individuals (%)		Shift in
	Untransformed	Transformed	ranking
Poaceae	40,2	43,9	1 / 1
Asteraceae	18,3	15,2	2 / 2
Fabaceae	8,4	7,3	3 / 3
Cyperaceae	2,9	3,1	4 / 4
Rubiaceae	2,3	2,2	5 / 6 $^{\vee 1}$
Acanthaceae	2,0	0,5	6 / 19 $^{\vee 13}$
Malvaceae	1,6	1,3	7 / 12 $^{\vee 5}$
Hyacinthaceae	1,5	0,1	8 / 47 $^{\vee 39}$
Commelinaceae	1,2	1,2	9 / 13 $^{\vee 4}$
Lamiaceae	1,2	0,3	10 / 28 $^{\vee 4}$
Verbenaceae	0,6	2,6	22 / 5 $^{\wedge 17}$
Amaranthaceae	0,2	2,1	47 / 7 $^{\wedge 40}$
Brassicaceae	0,1	1,9	50 / 8 $^{\wedge 42}$
Solanaceae	0,3	1,8	33 / 9 $^{\wedge 24}$
Myrtaceae	0,25	1,7	36 / 10 $^{\wedge 26}$

the weedy Amaranthaceae and Solanaceae benefitted in terms of species additions (9 and 5 species respectively; Table 1). Changes in the frequency of species is even more pronounced (Table 2). Five of the top ten families that have high frequencies of occurrence in untransformed grassland become reduced in transformed grassland by 73%. These are replaced by five families, which in turn showed a 75% increase in transformed grassland (Table 2).

Composition

Changes in the species number and frequency of families is expected to have an effect on the composition of transformed grassland. The results from a NMDS revealed clustering that supports the untransformed and transformed grasslands as separate assemblages (Figure 2). Results from the pair-wise tests in PERMANOVA indicated a significant difference in floristic composition between transformed and untransformed grasslands in both urban (df = 70, t = 2.17, p = 0.001) and agricultural (df = 70, t = 2.88, p = 0.001) transformation types (Figure 2). Bray Curtis similarity measures in the PERMANOVA design reported a low 6.96% and 5.7% similarity in species composition between transformed and untransformed agricultural and urban grasslands respectively. This implies that transformation changed species composition in grasslands by ~90% on average. Fifteen most common grass species explained 21.26% of the dissimilarity between transformed and untransformed grasslands, with species such as *Cynodon dactylon* and *Hyparrhenia hirta* weighted towards the former and *Digitaria eriantha* and *Themeda triandra* towards the latter (Table 3). Comparatively the first 15 forbs species only contributed 8.52% to the dissimilarity, with species such as *Cyperus esculentus* and *Richardia brasiliensis* weighted towards transformed, and *Helichrysum rugulosum* and *Scabiosa columbaria* towards untransformed grassland (Table 3).

Diversity

Changes in the species composition are expected to have an effect on species richness and diversity in transformed grassland. Simple paired t-tests revealed significantly lower diversity (for all measures, i.e. J', H', S and N) in the transformed grassland ($p<0.001$, Table 4). Species richness decreased by nearly 50%.

Status

The lower evenness in transformed grassland indicates uneven proportional contribution of individuals between species and is indicative of some species becoming more dominant and others becoming marginal. Dominance shifts can be ascribed to increased numbers of alien, invasive and annual species in the transformed grassland, with the former two being >80% lower in untransformed grassland (Table 4). Threatened and endemic species richness and abundance decreased by >80% in the transformed grassland (Table 4).

Growth forms

When aliens displace extant species (including endemics), certain growth forms become more or less prominent. Species losses (Table 4) were recorded for species with underground storage organs and bud-banks (USOs), such as geophytes (>80%), parasitic plants and suffrutices (>90%). Succulents were considered separately from the dwarf shrub growth form and were also decreased by over 90% in transformed grasslands (Table 4).

Discussion

Asteraceae and Fabaceae were the most dominant forb families in both transformed and untransformed grassland, a trend that has previously been reported (Botha et al. 2017). It can be deduced that regenerative traits, such as wind dispersal and seed dormancy for rapid colonisation (Asteraceae), ballochory and/or or endozoochory as seed dispersal traits, and resource acquisition traits, which increase resprouting capacity (Fabaceae), make them rather resilient to disturbance. However, the Amaranthaceae, Brassicaceae, Solanaceae and Verbenaceae benefit from the transformation of grasslands and their numbers and dominance increase through the introduction of weedy, mostly alien, species. These groups are renowned for their ability to colonise frequently transformed man-made habitats (Pysek, Prach & Smilauer 1995). In contrast, certain families, such as the geophytic Hyacinthaceae and Iridaceae, were extensively disadvantaged by habitat transformation, as they are sensitive to soil disturbance because their bud-banks are belowground (Fidelis et al. 2014). The general trend is therefore one of species loss and displacement by a new flora, mostly annuals, with colonising traits better suited to a transformed environment, such as creepers, clonal plants and fruit or seed adapted for exozoochorous or anemochorous dispersal (Botha et al. 2017).

Many species of ancient grasslands are not tolerant to anthropogenic disturbance (Siebert 2011). Common native species disappeared completely where grasslands were transformed, such as the grasses *Alloteropsis semialata* (R.Br.) Hitchc. and *Schizachyrium sanguineum* (Retz.) Alston, forbs *Gerbera ambigua* (Cass.) Sch.Bip. and *Haplocarpha scaposa* Harv., geophytes *Ledebouria luteola* Jessop and *Hypoxis argentea* Harv. ex Baker., dwarf shrubs *Athrixia phylicoides* DC. and *Tephrosia capensis* (Jacq.) Pers., and suffrutices *Elephantorrhiza elephantina* (Burch.) Skeels and *Ziziphus zeyheriana* Sond. Other species, such as the palatable and productive grass, *Themeda triandra*, which is considered a keystone species and indicator of undisturbed grassland (Snyman, Ingram & Kirkman 2013), were

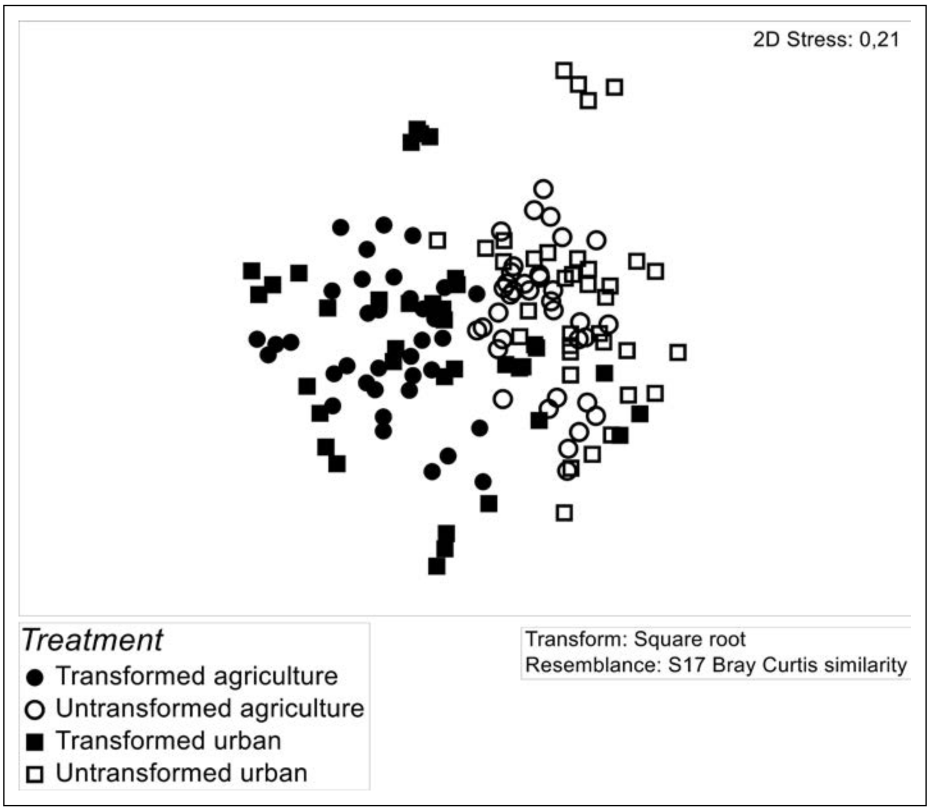

Figure 2: Non-Metric Multidimensional Scaling (NMDS) ordination for: A, transformed and untransformed grasslands; B, within land-use type transformation. Squares, transformed grasslands; circles, untransformed grasslands; Empty symbols, urban sites; filled symbols, agricultural sites.

Table 3. Similarity percentage analyses (SIMPER) of grass species contributing >0.6% to compositional differences between transformed and untransformed grasslands. Bold values indicate highest mean abundance. * denotes alien taxa. Superscripts: G, grass; F, forb

Species	Av.	Cont.	Cum.	Mean abundance	
	dis.	%	%	Transf.	Untransf.
Themeda triandra Forssk.^{G}	2.92	3.067	3.07	1.32	**13**
Cynodon dactylon (L.) Pers.^{G}	1.853	1.947	5.01	**7.85**	2.21
Eragrostis curvula (Schrad.) Nees^{G}	1.768	1.858	6.87	**5.63**	4.85
Eragrostis plana Nees^{G}	1.731	1.818	8.69	**5.13**	4.32
Hyparrhenia hirta (L.) Stapf^{G}	1.457	1.531	10.22	**5.35**	2.63
Digitaria eriantha Steud.^{G}	1.326	1.393	11.61	2.43	**4.93**
Setaria sphacelata (Schumach.) Moss^{G}	1.179	1.239	12.85	1.28	**4.89**
Aristida junciformis Trin. & Rupr.^{G}	1.148	1.206	14.06	0.74	**5.24**
Sporobolus africanus (Poir.) Robyns & Tournay^{G}	1.145	1.203	15.26	**4.79**	0.94
Eragrostis chloromelas Steud.^{G}	1.117	1.173	16.44	1.1	**4.56**
Pennisetum clandestinum Hochst. ex Chiov.^{G} *	1.115	1.172	17.61	**4.65**	0
Heteropogon contortus (L.) Roem. & Schult.^{G}	1.109	1.165	18.77	0.17	**5.07**
Tristachya leucothrix Trin. Ex Nees^{G}	1.014	1.066	19.84	0.9	**4.31**
Richardia brasiliensis Gomes^{F} *	0.755	0.793	20.63	**3.07**	0.35
Helichrysum rugulosum Less.^{F}	0.752	0.79	21.42	0.56	**3.25**
Eragrostis racemosa (Thunb.) Steud.^{G}	0.709	0.745	22.17	0.13	**3.1**
Cyperus esculentus L.^{F} *	0.695	0.73	22.89	**3.1**	0.04
Helichrysum nudifolium (L.) Less.^{F}	0.653	0.686	23.58	0.38	**2.86**
Eragrostis capensis (Thunb.) Trin.^{G}	0.648	0.681	24.27	0.33	**2.85**
Sisymbrium turczaninowii Sond.^{F}	0.637	0.67	24.94	**2.61**	0.15
Nidorella podocephala (DC.) Goldblatt & J.C.Manning^{F}	0.62	0.652	25.59	0.93	**2.17**
Hilliardiella oligocephala (DC.) H.Rob.^{F}	0.516	0.542	26.13	0.17	**2.26**
Tagetes minuta L.^{F} *	0.501	0.526	26.66	**2.18**	0.07
Scabiosa columbaria L.^{F}	0.487	0.511	27.17	0.38	**2.07**
Conyza bonariensis (L.) Cronquist^{F} *	0.484	0.509	27.68	**1.75**	0.4
Commelina africana L.^{F}	0.442	0.464	28.14	0.49	**1.78**
Felicia muricata (Thunb.) Nees^{F}	0.412	0.433	28.57	0.25	**1.61**
Plantago lanceolata L.^{F}	0.397	0.417	28.99	**1.57**	0.42
Bidens pilosa L.^{F} *	0.393	0.412	29.41	**1.68**	0.03
Zornia capensis Pers.^{F}	0.372	0.391	29.79	0.18	**1.6**

Av. dis.: Average dissimilarity; Cont. %: Contribution %; Cum. %: Cumulative contribution %; Transf.: Transformed; Untransf.: Untransformed. Distance/Similarity measure: Bray-Curtis.

severely reduced. Many new, mostly alien species, enter the transformed system, providing species that can be considered indicators of disturbance (Morris & Scott-Shaw 2019), such as the prostrate and grazing-resistant, *Richardia brasiliensis*. This study confirmed the results of O'Connor (2015) that a substantial decrease in *T. triandra* and increase in *R. brasiliensis* are indicative of transformed grassland.

As previously shown, untransformed grasslands have greater plant species diversity (27%) and richness (92%) than transformed grasslands (O'Connor 2005; Siebert

Table 4: Mean values (±SD) of selected diversity measures, growth forms, and alien, threatened and endemic species per plot. Percentage decrease is given in brackets. T-test results are reported for diversity measures, with significance set at $p < 0.05$

Measure	**Untransformed**		**Transformed**		**df**	**t**	**p**
Pielou's evenness (J')	**0.903** ±0.05		0.849 ±0.08	(6%)	142	4.92	<0.001*
Shannon Diversity Index (H')	**3.595** ±0.2		2.823 ±0.4	(21.5%)	142	13.93	<0.001*
Total species (S)	**54.7** ±10.2		28.5 ±7*	(47.9%)	142	17.9	<0.001*
Alien	0.9 ±1.1*	(87%)	**6.9** ±4.4				
Invasive	0.5 ±0.9*	(82.8%)	**2.9** ±3.2				
Threatened	**0.5** ±0.7		0.1 ±0.4*	(80%)			
Endemic	**6.7** ±3.2		1.3 ±1.4*	(80.6%)			
Annual	4.7 ±3.4*	(39%)	**7.7** ±5.4				
Perennial	**49.9** ±9.3		20.8 ±8.3*	(58.3%)			
Grass	**13.4** ±5.1		7.9 ±3.6*	(40.3%)			
Geophyte	**5.1** ±2.5		0.9 ±0.9*	(80.4%)			
Forb	**23.5** ±5.2		12.3 ±4.4*	(47.7%)			
Parasitic	**5.8** ±2.8		0.1 ±0.3*	(98.3%)			
Creeper	**1.6** ±1.3		0.9 ±1.2	(43.8%)			
Dwarf shrub	**6** ±2.7		1.6 ±1.3*	(73.3%)			
Succulent	**5.8** ±2.8		0.3 ±0.6*	(94.8%)			
Suffrutex	**5.8** ±2.8		0.1 ±0.4*	(98.3%)			
Tree/shrub	**5.9** ±2.7		4.2 ±6.2	(28.8%)			
Total individuals (N)	**286.7** ±64		167.3 ±40.8*	(41.6%)	142	13.36	<0.001*
Alien	3.6 ±6.9*	(90.4%)	**37.4** ±26.2				
Invasive	1.6 ±3.4*	(92.3%)	**20.8** ±22.9				
Threatened	**1.7** ±3.1		0.3 ±0.9*	(82.4%)			
Endemic	**29.2** ±17.1		7.4 ±15.1*	(74.7%)			
Annual	19.4 ±16.2*	(52.8%)	**41.1** ±36.3				
Perennial	**267.3** ±63.5		126.1 ±52.5*	(52.8%)			
Grass	**115.3** ±48.7		73.4 ±35.3*	(36.4%)			
Geophytic	**17.6** ±11.8		3.2 ±4.6*	(81.8%)			
Forb	**104.2** ±36.2		58.6 ±29.1*	(43.8%)			
Parasitic	**23.7** ±14.4		0.2 ±0.6*	(99.2%)			
Creeper	**5.3** ±6.4		3.1 ±4.1	(41.5%)			
Dwarf shrub	**24.8** ±14.1		5.9 ±7.8*	(76.2%)			
Succulent	**23.7** ±14.4		1.1 ±2.6*	(95.4%)			
Suffrutex	**23.8** ±14.4		0.2 ±1.7*	(99.2%)			
Tree/shrub	**24.1** ±14.1		21.5 ±27.6	(10.8%)			

2011). Species loss was specific to certain growth forms with underground organs specifically adapted to survive harsh winter conditions, drought and fire (Bond & Parr 2014; Bond 2016). The loss of these and other foundation species open up niches for colonisation by alien species (Prevéy et al. 2010). This is problematic, as loss of native species hampers the grassland ecosystem from fulfilling all its functions (Zavaleta et al. 2010). Overall, the situation in transformed grassland is not only one of species depletion, but increases in woody growth form dominance is predicted to become more pronounced in South African grasslands by 2030 (Gibson et al. 2018).

Conclusion

Major plant families remain floristically dominant after transformation, but there is a negative impact on overall phylogenetic diversity and the promotion of the Poaceae and Cyperaceae. Non-typical grassland families, with a wide array of disturbance-tolerant traits, show an increase in phylogenetic diversity, which is mainly a consequence of the introduction of alien weedy species.

Species composition of grassland was transformed by disturbance and is indicative of better adapted species entering the system or existing pre-adapted ones becoming more dominant due to competition release and/or altered microclimates and soils (Pysek, Prach & Smilauer 1995). This is evidenced by the proportion of grass species increasing, but a large reduction in forb species with USOs (Fidelis et al. 2014). No evidence was found for extensive woody encroachment in transformed areas.

This study set out to assess species loss due to transformation and, based on the current data set, it can be conclusively stated that grassland is severely impacted in terms of its species richness and diversity. These changes are of concern as grasslands have high economic value and support the wellbeing of humans by providing, among others, ecological infrastructure, carbon sinks, albedo surfaces, plant-based medicines, food plants and grazing for livestock (Bengtsson et al. 2019). Further studies are needed to determine whether these floristic shifts can still maintain and provide the ecosystem services that are expected from grasslands in South Africa.

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Authors’ contributions

MM collected field data, conducted data analyses and contributed to the writing of the manuscript. SJS planned and coordinated the study, collected field data, conducted data analyses and co-wrote the manuscript. BRN planned and coordinated part of the study, collected field data, and conducted data analyses. FS collected field data and contributed to the writing of the manuscript.

Disclaimer

The views expressed in the submitted article are our own and not an official position of the institution or funder.

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Open Ecosystems:
Ecology and Evolution Beyond the Forest Edge

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By William Bond

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Background

This book represents the pinnacle of research outputs by author William Bond and strongly reflects his long standing passion for non-forested, open ecosystems ecology. For decades, Bond aspired to solve ecological problems (Leonard 2012), and this insatiable curiosity has shaped him into an internationally acclaimed plant ecologist. In his latest book, he challenges global misconceptions on the antiquity of natural open ecosystems, which have led to poorly conceived global policies to reforest them (Silveira et al. 2020). Furthermore, the content of the book challenges long-held concepts in ecology, biogeography and paleoecology, but with remarkable scientific evidence and support across the global extent of open ecosystems. With no surprise, the author's extensive knowledge of and interest in fire as key driver of vegetation dynamics features across all sections related to fundamental questions of where, why and for how long open ecosystems occur side-by-side with closed forest ecosystems.

Open ecosystems (OEs), in the context of this book, refer to all grasslands, savannas and shrublands globally, which occur in climates that are warm and wet enough to support closed forest ecosystems, and yet they are not forests, and certainly do not represent anthropogenically induced degraded forests. The aim of the book is to present general explanations for the existence of OEs. Providing authoritative support for their existence is envisioned to assist in the differentiation between ancient old-growth, and secondary OEs, which are products of deforested landscapes. Proper differentiation between ancient and secondary OEs is critical in the current ecological restoration age where several internationally supported policies and funding bodies are engaged with global afforestation campaigns. Such restoration plans expand deeply into ancient OEs worldwide due to general misconceptions on the antiquity and ecological functioning of these fascinating uncertain ecosystems (Bond 2016). In my view, the book provides a strong base that allow ecologists to acquire further evidence to support the existence, evolutionary history, ecological functioning and biogeography of OEs. For an expertly conducted technical review of the book, see O'Connor (2019).

Content of the book

The book contains nine chapters, full references as well as an index to key words and key concepts, which facilitate quick referencing to particular topics when using a hard copy. The introductory chapter sets out a general explanation of OEs, supported by Fynbos shrublands as an example, presumably due to the author's deep interest and research experience in this ecosystem type. The introduction chapter is well-structured and includes the scope of what will be covered. Not only is the reader well prepared on OE ecology, which is provided through a strong overview of the history of global ecological research, but current advanced technologies and contemporary ecological theory are introduced, and their value and application highlighted for future support of OEs' existence. Four ensuing chapters respectively explain climate patterns, ecological drivers, vegetation dynamics and evolutionary history of OEs and how these are interrelated to a central explanation of the antiquity of non-forested OEs.

The 'climate-physiognomy classification of vegetation' assumption is challenged in the first chapters of the book. Taking the reader through examples of vegetation–climate correlation studies from the tropics, to temperate and boreal ecosystems, the book introduces the origin of a common fallacy that OEs are degraded forests. Although not being elaborated upon much, the author agrees that climate extremes, such as drought and frost, seem to be more important than average climate conditions in explaining OE structuring. Climate is only but one of the ecologically important drivers being discussed in detail. Soil properties, which are discussed in more detail later in the book (Chapter 6), are presented as another traditional explanation for OEs. From a summary section in this chapter, research on below-ground processes and plant-soil feedbacks seems to be limited. Yet, there seem to be no fixed, optimal explanation of ecosystem ranges based on basic drivers, such as climate and soil alone, as some ecosystems associated with certain climates and substrates may support multiple stable states. For this reason, the book introduces the reader to unconventional explanations of OEs, such as large-scale consumer control, including fire (Chapter 7) and vertebrate herbivory (Chapter 8) in the context of alternative stable states. Well-structured discussions on each of the above, supported with examples from different continents, are captivating, as they broaden the ecological understanding of OEs.

Providing a convincing explanation for the evolutionary origin of OEs remains challenging. This book, particularly Chapter 5, presents an informative evolutionary background of OEs. What I found particularly interesting, was the role of long-term interactions, such as climate and CO_2, with consumers such as mammals and fire, in shaping current OEs. Since these interactions are complex and dynamic, I feel a single, explanatory diagram indicating clear distinctions and overlaps of all evolutionary drivers and consequences across geological time, would have been a valuable addition to Chapter 5 to summarise the in-depth context.

To me, Chapter 4 ('The nature of open ecosystems') was the most intriguing read in the book. Through global perspectives of OEs' diversity, endemism, antiquity and functional adaptations, this chapter provides a concise summary of the origin and extent of the exceptionally rich nature of OEs. The final chapter not only summarises the key threats to OEs in the context of global change, but particularly highlights important knowledge gaps and opens up new research questions and perspectives. This has already inspired a research agenda for the restoration of OEs (Buisson et al. 2020).

Overall, the book has few weaknesses. *Open Ecosystems* was a fascinating read, packed with authoritative evidence, personal observations and experimental support across the globe. The content makes out, and often challenges, a solid body of past and novel ecological hypotheses, presented in a rather coherent manner. The ultimate strength of this book is that it clearly defines research gaps and provides important guidelines for future research aimed at an improved understanding of OEs. Building upon such foundations, OE ecologists are better equipped to motivate for the conservation of its biodiversity, function and services beyond quick-fix attempts to combat global climate change.

The book showcases OEs as ancient ecosystems, persisting for millennia through creating their own preferred environmental conditions. Someday, I think, the world will 'lift their heads in awe at the ways in which life is organized as a collective in diverse parallel worlds' – quoted from Chapter 3 (section 3.10, p. 42). The responsibility now lies on current and future OE ecologists to change the aftermath of the very last sentence of this book 'Maybe it is not too late', to 'It came at the right time and surely was not too late'.

Disclaimer: This article was not peer reviewed.

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Guidelines for authors

These guidelines provide an overview of the structure and style of articles to be submitted to the South African National Biodiversity Institute (SANBI)'s peer-reviewed journal:
Bothalia – African Biodiversity & Conservation.

TYPES OF ARTICLES

Full length articles report on complete, comprehensive pieces of original research, as well as reviews, strategies or innovative case studies in any field of work aligned with the scope of the journal. Full length articles include a maximum of 8 000 words and 60 references.

Short communications are concise reports on narrow investigations. These include new species descriptions. They have a maximum of 2 000 words and 30 references.

In the case of reviews, strategies and short communications, not all of the headings and subheadings specified below may be relevant. In such cases authors will need to use their discretion in selecting appropriate headings.

FORMATTING

Manuscripts must be submitted as a MS Word document. Documents compiled in other software, including Google Documents, cannot be accepted.

Low resolution versions of figures and tables can be inserted into the document. High resolution of figures must, however, also be included separately, with each figure as a separate, appropriately labelled file (see details of requirements for figures below).

Please do not use hidden formatting, including character styles in the manuscript. Also avoid nested tables and text boxes. Many of these cause corruptions in the design software, and can usually be avoided if authors refrain from copying and pasting from various sources, including other MS Word documents.

- **Language:** Manuscripts must be written in British English. Avoid Americanisms (e.g. use 's' and not 'z'). Consult the Oxford English Dictionary when in doubt and remember to set your version of Microsoft Word to UK English.
- **Line numbers:** Insert continuous line numbers.
- **Font:**
  - **Font type:** Times New Roman
  - **General font size:** 12pt
- **Line spacing:** 1.15
- **Headings:** Ensure that formatting for headings is consistent in the manuscript.
  - First headings: normal, bold and 14pt
  - Second headings: normal, bold and 12pt
  - Third headings: normal, underlined and 12pt
  - Fourth headings: normal, bold, running-in text and separated by a colon, and 12pt.

Scientific names: Names of genera and infrageneric taxa are italicised, with the author citation not italicised. Exceptions include specific cases in taxonomic treatments (see details of such manuscripts below); new taxa in the abstract; and in checklists where the position is reversed – correct names are not italicised and synonyms are italicised. Names above generic level are not italicised. The complete scientific name of a species as well as the author citation should be given at the first mention in the text. The generic names should be abbreviated to the initial thereafter, except where references to other genera with the same initial could cause confusion.

Authors of botanical names are abbreviated according to Authors of Plant Names (Brummitt & Powell 1992, Royal Botanic Gardens, Kew).

In names covered by the International Code of Zoological Nomenclature, the date of publication should be separated from the authority by a comma (e.g. *Anthomyza bellatrix* Roháçek, 1984). When a species or subspecies is transferred to a genus other than that in which it was first classified, the original authority, including the date, is placed in parentheses.

Adjectives and nouns derived from genus names become Roman with a lower case initial (e.g. *Felis*→feline, *Libellula*→libellulids, *Streptococcus*→streptococcal infection).Those derived from higher taxonomic groups also begin with a lower case letter and are presented in Roman (e.g. Ostracoda→ostracods, Cactaceae→cacti).

A scientific name given at its first mention after a vernacular name should be separated from it by a comma if the two names are exact synonyms (e.g.…the two-spotted cricket, *Gryllus bimaculatus*,…), but not if the vernacular name may apply to more than one species (e.g. the starfish *Asterina pectinifera*, the medaka *Oryzias latipes*).

Abbreviations should be used sparingly but consistently. No full stops are placed after abbreviations ending with the last letter of the full word, after units of measure, after compass directions, after countries and after well-known institutions.

FIGURES AND TABLES

The word Figure should be written out in full and should begin with a capital F, in both the text and captions.

Figures (original or electronic submissions):

- Figures should be planned to fit, after reduction, into a width of either 80, 118 or 165 mm, with a maximum vertical length of 230 mm. Allow space for the caption in the case of figures that will occupy a whole page.
- Graphics, i.e. drawings, graphs or photographs, should be submitted as separate files. Low resolution copies of the figures should be included in the manuscript for review purposes.
- If extensive changes to image files are proposed by the editor, the author will be contacted and the specific image file will have to be re-submitted after the indicated corrections have been implemented.
- Scale bars or scale lines should be used on figures where relevant.
- Captions should not be added as part of the figure file. Number captions clearly and correctly and include either in the main text close to where the figure should be inserted or as a list of captions at the end of the text; not as a separate document.
- Authors wishing to use illustrations already published elsewhere must obtain written permission before submitting the manuscript and provide this to the editor at the time of submission, along with appropriate acknowledgements.
- Do not resample low resolution images to a higher resolution.
- Mosaics should be submitted as separate photographs as TIF/JPG files at 600 dpi or higher. A mockup of the layout should also be submitted. Final layout of the mosaic will be done by our graphics department. Do not number the original images, but do include a scale bar. Indicate the lettering on the mockup and not on the original photographs.
- Manuscripts for which the figures, including line drawings, photographs, graphs and histograms, and maps, do not comply will be rejected for design and layout, even though the paper was accepted for publication, until such time that the authors can provide suitable images. This can significantly delay publication.

Line drawings:

- The original artwork should be in jet-black Indian ink, on fine art paper, 200 gsm. Lines should be clear enough to accommodate reduction. Do not use draughtman's film.
- Drawings in pencil will not be accepted.
- Provide original drawings electronically as bitmap TIF files, 1200 dpi.
- At the request of the author, the Graphic Design Section of SANBI will assist with the scanning of original material. Authors wishing to have the originals of figures returned must inform the editor in writing and mark each original 'To be returned to author'.

Photographs:

- Provide photographs electronically as either TIF or JPG files, 600 dpi or higher.

Graphs and histograms:

- The typeface for all graphs and histograms is Arial.
- Provide graphics originated in CorelDraw (version 16 or lower), as a .CDR file.
- Graphs and histograms generated in MS EXCEL or MS Word, should be provided as is. File conversion into the correct format will be accommodated by SANBI Graphics.
- Images generated in other programmes should be submitted as TIF or JPG files at a resolution of 600 dpi or as encapsulated postscript files (.EPS). If graphs and histograms are submitted in colour, please ensure that the shading used is easily discernible once the file is converted to grayscale.

Maps:

- It is strongly recommended that taxonomic articles include dot maps as figures to show the distribution of taxa. If maps will be reduced to column width (80 mm), the symbols and numbers used must be large enough to accommodate the reduction. The maps should show: numbered grid lines of latitude and longitude; the provinces of South Africa; and a scale line. Maps of neighbouring countries should be treated in the same way, with bordering states clearly labelled. For orientation purposes, a small inset map should appear in a corner of the figure.
- Submit maps electronically as either TIF or JPG files, 600 dpi or higher.
- ArcView GIS maps are acceptable. The layout representing all the appropriate themes (including grid lines) should be submitted as an encapsulated postscript file (.EPS).
- If maps are submitted in colour, please ensure that the shading used is easily discernible once the file converted to grayscale.

Tables:

- Tables should be drawn up in MS Word and not copied and pasted from other software such as MS Excel.
- Avoid copying and pasting text into the table as this often result in nested tables that are problematic to format and edit. Type in all text from scratch.

- Do not submit tables as text with separators such as tabs or commas, submit as MS Word standard tables.
- Do not include text boxes in table cells, type text directly in the primary table cell.
- Use Times New Roman 12pt if possible. However, should the width of the columns and the amount of text make this difficult, the size of the font may be reduced to no less than 9pt.
- If possible, present tables in portrait format. However, if tables must be presented in landscape format, use section breaks before and after the tables to separate it from the main text.
- Do not stretch the table to beyond the size of the paper on screen.
- Use the background fill function to shade cells if necessary. Do not use text highlights.

STRUCTURE OF YOUR ARTICLE

Page 1:

The format of the compulsory cover letter forms part of your submission and is on the first page of your manuscript and should always be presented in English. You should provide all of the following elements:

- **Article title:** Provide a short title of 50 characters or less.
- **Full author details:** Provide title(s), full name(s), position(s), affiliation(s) and contact details (postal address, email, telephone and cellular number) of each author.
- **Corresponding author:** Identify to whom all correspondence should be addressed to.
- **Authors' contributions:** Briefly summarise the nature of the contribution made by each of the authors listed.
- **Summary:** Lastly, include a list containing the number of words, pages, tables, figures and/or other supplementary material with the submission.

Page 2 and onwards:

Title: The article's full title should contain a maximum of 95 characters (including spaces).

Abstract: The abstract, written in English, should be no longer than 250 words and must be written in the past tense. The abstract should give a succinct account of the background, objectives, methods, results and significance of the findings/conclusion

Do not cite references in the abstract and do not use abbreviations excessively in the abstract.

The following points serve as a guide for presenting your manuscript in a well-structure format:

Introduction: The introduction contains two subsections, namely the background section and the literature review.

- **Background:** This section should be written from the point of view of the readers, including those without specialist knowledge in that area and must clearly state and illustrate the introduction to the research and its aims in the context of previous work bearing directly on the subject. The Background section to the article normally contains the following five elements:
    - ○ **Key focus:** A thought-provoking introductory statement on the broad theme or topic of the research.
    - ○ **Context:** Provide the context to the study, which can include the conceptual framework or explain the role of other relevant key variables in this study.
    - ○ **Trends:** Cite the most important published studies previously conducted on this topic or that have any relevance to this study (provide a high-level synopsis of the research literature on this topic).
    - ○ **Objectives:** Indicate the most important controversies, gaps and inconsistencies in the literature that will be addressed by this study. In view of the above trends, state the core research problem and specific objectives that will be addressed in this study.
    - ○ **Contribution to field:** Explanation of the study's academic (theoretical and methodological) or practical merit and its importance (provide the value-add or rationale for the study).
- **Literature review:** The literature review is the second subsection under the Introduction and provides a brief and concise overview of the literature under a separate second-level heading, e.g. literature review. A synthesis and critical evaluation of the literature (not a compilation of citations and references) should at least include or address the following elements (ensure these are in the literature review):
    - ○ Definitions of all key concepts.
    - ○ A critical review and summary of previous research findings (theories, models, frameworks, etc.) on the topic.
    - ○ A clear indication of the gap in the literature and for the need to address this void.
    - ○ A clearly established link that exists between formulated objectives and theoretical support from the relevant literature.

Research method and design (first-level heading):

The methods should include:

- **Materials (second-level heading):** Describe the type of organism/s or material/s involved in the study.
- **Study site (second-level heading):** Describe the site and setting where your study was conducted.
- **Design (second-level heading):** Describe your experimental design clearly. Note: Additional details can be placed in the online supplementary location.
- **Procedure or Methods (second-level heading):** Describe the protocol for your study in sufficient detail (with a clear description of all interventions and comparisons) so that other scientists could repeat your work to verify your findings.

- **Analysis (second-level heading):** Describe how the data were summarised and analysed. Additional details can be placed with the online supplementary information. Do not include lists here as they will be published as supplementary material.

Ethical considerations (first level heading):

- **Ethical clearance (second-level heading):** Articles based on the involvement of animals and/or humans must have been conducted in accordance with relevant national and international guidelines. Approval must have been obtained for all protocols from the author's institutional or other relevant ethics committee and the institution's name and any ethics certificate number/s should be provided at submission.
- **Risks or negative impacts associated with research and mitigation (second-level heading):** This section should consider any risks or negative impacts to the subjects caused by the project (the subject may be a human individual or a population of plants or animals). What precautions were taken to minimise any negative impacts of the research on the subject/s?
- **Permitting (second-level heading):** Projects that required permits for collection, transport or provision of material must provide all relevant permit details.
- **Recruitment and informed consent (second-level heading):** In the case where human subjects were involved, how were subjects recruited? Was there any sense in subjects being obliged to participate or were volunteers recruited. Authors must include how informed consent was handled in the study.
- **Data protection (second-level heading):** Authors must include, in detail, the way in which data protection was handled.

Results (first-level heading):

Results should be presented as follows:

- Present the results of your experiment(s) or research data in a sequence that will logically support (or provide evidence against) the hypothesis, or answer the questions / address the objectives, as stated in the introduction.
- Present the body of the results section in text with the key findings that include references to each of the tables and figures. Report statistical test summaries (test name, p-value) parenthetically (that is, inserted as a parenthesis in brackets) together with the biological results they support. Use the SI unit.
- All units should conform to the SI convention and be abbreviated accordingly. Metric units and their international symbols are used throughout, as is the decimal point (not the decimal comma).

Discussion (first-level heading):

This section normally contains the following four elements. It is suggested that subheadings are used in this section:

- **Outline of the results (second-level heading):** Restate the main objective of the study and reaffirm the importance of the study by restating its main contributions; summarise the results in relation to each stated research objective or research hypothesis; link the findings back to the literature and to the results reported by other researchers; provide explanations for unexpected results.
- **Practical implications (second-level heading):** Reaffirm the importance of the study by restating its main contributions and provide the implications for the practical implementation your research.
- **Limitations of the study (second-level heading):** Point out the possible limitations of the study and provide suggestions for future research.
- **Recommendations (second-level heading):** Provide the recommendations emerging out of the current research.

Conclusion (first-level heading):

This should state clearly the main conclusions of the research and give a clear explanation of their importance and relevance, with a recommendation for future research (implications for practice). Provide a brief conclusion that restates the objectives, the research design and the results with their meaning.

Acknowledgements (first-level heading):

If, through your study, you received any significant help in conceiving, designing or carrying out the work, or received materials from someone who did you a favour by supplying them, you must acknowledge their assistance and the service or material provided. *Authors should always acknowledge outside reviewers of their drafts and any sources of funding that supported the research.*

- **Competing interests (second-level heading):** A competing interest exists when your interpretation of data or presentation of information may be influenced by your personal or financial relationship with other people or organisations that can potentially prevent you from executing and publishing unbiased research. Authors should disclose any financial competing interests, but also any non-financial competing interests that may cause them embarrassment were they to become public after the publication of the manuscript.

  > *Where an author gives no competing interests, the listing will read:*
  >
  > 'The authors declare that they have no financial or personal relationship(s) that may have inappropriately influenced them in writing this article.'

- **Authors' contributions (second-level heading):** This section is necessary to give appropriate credit to each author, and to the authors' applicable institution/s. The individual contributions of authors should be specified with their affiliation at the time of the study and completion of the work. An 'author' is generally considered to be someone who has made substantive intellectual contributions to a published study. Contributions made by each of the authors listed, can follow the example below (please note the use of author initials):

> J.K. (University of Pretoria) was the project leader, L.M.N. (University of KwaZulu-Natal) and A.B. (Stellenbosch University) were responsible for experimental and project design. L.M.N. performed most of the experiments. P.R. (Cape Peninsula University of Technology) made conceptual contributions and S.T. (University of Cape Town), U.V. (University of Cape Town) and C.D. (University of Cape Town) performed some of the experiments. S.M. (Cape Peninsula University of Technology) and V.C. (Cape Peninsula University of Technology) prepared the samples and calculations were performed by C.S. (Cape Peninsula University of Technology).

References (first-level heading):

Begin the reference list on a separate page with no more than 60 references for full length articles and 30 references for short notes. The *Bothalia – African Biodiversity & Conservation* Journal uses the **Harvard referencing style**. Note: no other style will be permitted.

If you use any reference editor to add citations in the text, remove all data fields and replace with normal text before submission.

For journal articles, provide DOIs for as many as possible (usually all papers published in or after 2000). The DOI reference can be provided after a comma at the end of each reference.

TAXONOMIC PUBLICATIONS

Bothalia – African Biodiversity & Conservation publishes taxonomic findings where these align with the scope and focus of the journal (see Scope and Focus of *Bothalia – African Biodiversity & Conservation*). For such works the following headings should be used:

The Abstract and Introduction must follow the guidelines for full length articles, as described above.

Research method and materials (first-level heading):

- **Materials (second-level heading):** Briefly explain from which institutions material was studied, and whether any fresh material was collected as part of the study. If field collecting did take place explain where this was carried out, over what time period and how samples were collected.
- **Procedure (second-level heading):** Explain how observations, measurements and illustrations were done, and what equipment was used.

Taxonomic treatments (first-level heading):

This section serves as a guide to understand and standardise the presentation of taxonomy in research articles and short communications.

More details of rules that must be adhered to can be obtained from:

- The International Plant Names Index at http://www.ipni.org/
- International Association for Plant Taxonomy at http://www.iapt-taxon.org/
- The International Commission for Zoological Nomenclature (http://www.iczn.org)

The following sequence and format must be followed for taxonomic treatments in *Bothalia – African Biodiversity & Conservation*:

Species treatments:

- Basionym (the first name validly published, which has priority over other names later given to the same species): **Name** (bold, not italicised), *author citation* (italicised), author/s of paper in which basionym stated (if different from original author, not italicised).
- Name of the journal/publication written out in full (not italicised), volume: page number/range (date of publication), fig/s.
- Type locality: COUNTRY (upper case), as provided in the original description. Type specimen/s: date of collection, *collector (italicised), collector number* (italicised) (where available), institution code (using global acronym), catalogue number (where available), status (holotype, isotype/syntype, lectotype). If specimen was examined, this is indicated by a '!' after the specimen status.
- Additional references, in chronological order, with author: page (year of publication), figure number/s reflected (e.g. Boris et al.: 14 (1966); Boris: 89 (1967), fig. 9.).
- List of synonyms in chronological order, arranged in groups of nomenclatural synonyms (i.e. homotypic synonyms (based on the same type), followed by heterotypic synonyms (based on a different type), arranged chronologically), with references cited as author, page (year of publication), and figure number/s listed in chronological order.
- Identification of illegitimate names in the nomenclatural component must be accompanied by an appropriate indication of the reason for their illegitimacy. The type details for each heterotypic synonym should be included (institution code followed by catalogue number where available and type status), and those specimens examined by the author/s

must be indicated by an exclamation mark. The full reference for citations must be included in the Reference List.

Examples:

1. **Eremiolirion amboense** (*Schinz*) *J.C.Manning & C.A.Mannheimer* in Bothalia 35: 117 (2005), fig. 4. Type: South West Africa [NAMIBIA], Amboland [**Ovamboland**], Ongangua [Ondongwa], without date, *Ruatanen 344* (Z.holo!).

2. **Walleria gracilis** (*Salisb.*) *S.Carter* in Kew Bulletin 16: 189 (1962). *Androsyne gracilis* Salsb.: 61 (1866). Type: SOUTH AFRICA, **Western Cape**, *William Marsden* [BM, holo!; drawing in Salisbury mss.8: 818 (BM)].

   W. armata Scltr. & K.Krause in Krause: 235 (1921). Type: SOUTH AFRICA, [**Western Cape**, near Klawer], [Farm] Windhoek, 8 July 1896, *R. Schlechter 8074* (B, holo [not seen]; BM!, BR!, COI!, GRA!, K, MO!, PRE!, S!. iso).

3. **Plagiotaphrus improvisus** *(Attems 1934) Hoffman* in Revue de Zoologie et de Botanique Africaines, 83 (3–4): 209 (1971), fig. 2. *Megaskamma improvisa:* Attems: 16: 13 (1934), figs 14–17. Type: **ANGOLA**, near Cuanza River, Biėi District, Jan. 1932, *F. Haas* (SMF 1694, holo. [not seen] 1 male).

- Lectotypes or neotypes should be chosen for correct names without a holotype. It is not necessary to lectotypify synonyms. When a lectotype or neotype is newly chosen, this should be indicated by using the phrase “here designated”. If reference is made to a previously selected lectotype or neotype, the name of the designating author and the literature reference should be given. In cases where no type was cited, and none has subsequently been nominated, this may be stated as “not designated”.

Description of new taxa:

- All newly described taxa and newly proposed synonyms and new combinations should be explicitly designated as such, e.g. fam. nov., trib. nov., gen. nov., sp. nov., nom. nudem., syn. nov., comb. nov.

Name (bold, not italicised) sp. nov. authority (if different to the authors of the manuscript)

TYPE/S: (holotype followed by paratype/s) (COUNTRY (upper case), **province** (bold), locality as given by original collector (if in foreign language or using archaic or outdated place names then these must be placed in inverted commas, with modern equivalent of collecting locality in square brackets (if relevant)), geographic co-ordinates (if the geographic co-ordinates were not provided on the specimen label or provided by the collector, and were identified by the author using a gazetteer or Google Earth, this must be indicated by including the co-ordinates in square brackets, altitude, habitat or other available, relevant collecting details, date of collection, *collector’s name (italicised), collector’s number (italicised)* (if available), (institution where specimen is housed (using global acronyms for these), catalogue number (if available), number of specimens by male and female (where relevant)).

Examples

1. **Lasiosiphon rigidus** J.C.Manning & Boatwr., sp. nov.

   TYPES: SOUTH AFRICA, **Northern Cape**, Tankwa [Tangua] Karoo National Park, SW foot of Leeuberg, along drainage lines, [32°18,2’S / 20°0.3’E, 414 masl], 20 Jun. 2012, *Manning 3363* (NBG, holo., MO, PRE, iso).

2. **Doratogonus microsetus** sp. nov.

   TYPES: SOUTH AFRICA, **Mpumalanga**: Wakkerstroom, 27.36670°S / 30.01670° E, 20 Dec, 2000, *D. Forbes (*NMSA 21786, 1 male holo.; NMSA 21787, 2 males, 1 females, para.).

Second-level headings for taxonomic treatments:

- Description (with third-level headings if required, and according to diagnostic characters for the particular taxon)
- Distribution and habitat
- Ecology
- Etymology
- Local name/s
- Uses / economic value
- Diagnosis and relationships
- Conservation status – comment on whether included in existing Red Lists, or whether the species would potentially qualify as threatened and describe current and potential threats.
- Other material examined (country (upper case), province (bold): locality as given by original collector, modern equivalent of collecting locality in square

brackets (if relevant), co-ordinates (degrees, minutes decimal) (in square brackets if gazetteer or Google Earth used by author), approximate altitude, date of collection, *collector's name (italics), collector's number* (italics) (if available) (institution where specimen is housed (using international acronym or code for these), catalogue number (if available), number of specimens by male and female (where relevant)).

- List of specimens must be arranged alphabetically by country, and within countries, by province in alphabetical order, and within provinces, alphabetically by locality name, and as far as possible keeping those specimens from the same locality together, then in chronological order by collection date.
- Herbarium acronyms follow Index Herbariorum [Thiers, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/]. The accepted acronyms for other institutions can be obtained from the Global Registry of Biorepositories (GRBio) (http://grbio.org).
- Original locality information in a foreign language or using archaic/outdated place names should be indicated using inverted comas, with any relevant corrections for modern usage, including conversions to metric units, added in square brackets.

The date of collection is to be presented as day, month of the year (abbreviated as Jan., Feb., Mar., Apr., May, Jun., Jul., Aug., Sept., Oct., Nov., Dec.), and year in full.

Geographic co-ordinates must be presented as taken from a GPS, or from an online gazetteer or georeferencer in degrees, decimal minutes (DDM). Records must also indicate the hemisphere (E or W and N or S, and the estimated/approximate altitude. If the geographic co-ordinates and approximate altitude were not provided on the specimen label or provided by the collector, and were identified by the author, this must be indicated by including the co-ordinates in square brackets.

For species that may be threatened by over-collecting, the co-ordinates can be degraded to reflect only the degrees and minutes. In the case of old specimens where the exact locality is unknown the degree and minutes or equivalent, or the degree or quarter degree grid square can be provided.

Examples:

1. SOUTH AFRICA. **Western Cape**: Near Eendekuil, western foot of Piekenierskloof Pass, [32°37.136'S / 18°57.525'E 476masl], 28 Aug. 2009, *Magee, Boatwright, Manning and Goldblatt 161* (NBG, PRE, K, BOL); roadside near Gouda, [33°37.136'S / 19°2.044'E, 85masl], 09 Sept. 1951*, Esterhuysen 18840* (BOL [3 sheets], K, PRE).Tulbagh, 33°17.126'S / 19°8.257"E, 162masl, Sept. 1919, *Bolus 16734* (BOL);
2. SOUTH AFRICA: **KwaZulu-Natal:** Nkandhla Forest, in forest along dirt road, 28º43'38.592"S / 31º07'58.281"E, 1121 masl, 19 Nov, 2001, *A. Armstrong & H. Murray* (NMSA 21970 [1 male, 1 female]).

Language for these sections must be as concise as possible, using principles instead of verbs.

The remaining first-level headings (Discussion, Conclusions, Acknowledgements, Competing interests, Authors' contributions and References) must follow the same format as for full length articles, as detailed above.

Images – low resolution version in the text file; high resolution files – correctly labelled – as separate JPG, TIF or EPS files.

Identification keys: Dichotomous keys must use sequential numbering, with the two parts of the couplet numbered 1a, b; 2a, b etc. New species included in keys must be bolded and not italicised, and sp. nov. must be stated, while other species names must not be bolded, must be italicised, and must include the species authority in the correct format.

Illustrations for taxonomic works: Descriptions of new plant species should include a photograph of the holotype specimen, unless there is a good reason for not providing this. For all taxa, descriptions of new species and taxonomic revisions should include annotated illustrations that clearly show and indicate diagnostic characters.

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Bothalia – African Biodiversity & Conservation will accept notes on nomenclatural changes. Authors are encouraged to include all name changes into a single manuscript and not to split these into separate manuscripts. Note that where a nomenclatural changes are a formality, and not based on research findings presented, the manuscript may not be subjected to a full review process. In such cases the publication will clearly state that the paper has not been peer reviewed.

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