BOTHALIA –
African Biodiversity & Conservation

ISSN: 0006-8241

Volume 54. 2024

SANBI
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South African National Biodiversity Institute

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A peer-reviewed publication of the
South African National Biodiversity Institute

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Bothalia – African Biodiversity and Conservation is published by the South African National Biodiversity Institute (SANBI), a government funded entity under the Department of Forestry, Fisheries & the Environment.

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Website: http://abcjournal.org
General enquiries: editorialboard@abcjournal.org
ISSN: 2311-9284 (Online)
ISSN: 0006-8241 (Print)

Obtainable from: SANBI Bookshop, Private Bag X101, Pretoria, 0001 South Africa.
Tel.: +27 12 843 5000
E-mail: sanbibookshop@sanbi.org.za
Website: www.sanbi.org
Printed by: Shereno Printers, 10 Atlas Road, Dunswart, Boksburg, South Africa; website: www.shereno.co.za

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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.

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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.

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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.
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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.

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Bothalia – African Biodiversity & Conservation, Vol. 52, Issue 1.

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ISSN: (Online) 2311-9284, (Print) 0006-8241

Revision of the North West province, South Africa, vegetation map

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Dates

Submitted: 24 October 2023
Accepted: 12 April 2024
Published: 11 October 2024

How to cite this article:

Desmet, P.G., Hawley, G., Dayaram, A, Power, R.J., Heydenrych, R., Dzerefos, C.M., Schaller, R., Hahn, N., Job, N., 2024, 'Revision of the North West province, South Africa, vegetation map', *Bothalia* 54, a10. http://dx.doi.org/10.38201/btha.abc.v54.10

Background: The vegetation type boundaries in the North West province as they appear in the 2018 National Vegetation Map, for the most part, are derived from agricultural land types that were mapped in the 1980s.

Aim & objectives: Given (1) the importance the National Vegetation Map plays in conservation assessment and planning, as well as environmental planning and decision making; and (2) the map boundary errors reported by users, an update of the provincial vegetation map was considered necessary.

Methods: A vegetation identification key using high-level environmental parameters (in order of importance: flooding, bioregion, terrain, geology and soil) was developed. This key was used to manually interpret high-resolution colour aerial imagery, together with existing environmental spatial datasets (land types as a proxy for soils, simplified geology and terrain/land form). The existing vegetation type concepts are sound and are mostly retained in this map.

Results & conclusion: Changes to the map include: (1) all vegetation boundaries in the province are remapped; (2) Olea Sclerophyllous Forest is proposed as a sub type/community related to the Northern Afrotemperate Forest vegetation type; (3) two existing vegetation types currently not mapped as occurring in the province are brought into the province, namely, Subtropical Alluvial Vegetation and Waterberg Mountain Bushveld; and (4) three vegetation units recognised in previous vegetation studies and which are not indicated in the current National Vegetation Map are included here as new vegetation types, namely, Vryburg Thornveld, Morokweng Thornveld and Central Sandy Mountain Bushveld. The descriptions of all terrestrial vegetation types occurring in the province are also updated and an updated annotated global plant species list for the province is provided. Changes reflected in this vegetation map have been incorporated into the National Vegetation Map Version 2024 beta.

Keywords: North West, vegetation map, classification, ecosystem type, revision.

Introduction

The South African vegetation map is a national scale map of the terrestrial ecosystems found within the country. The current National Vegetation Map, first published in 2006 (Mucina & Rutherford 2006) and updated in 2018 (Dayaram et al. 2019), includes 459 unique vegetation types of which 35 terrestrial and six azonal types occur in the North West province (NW). A beta release of the next version was released in 2024 (SANBI 2006–2024), which now incorporates revisions from work in this paper.

The purpose of the National Vegetation Map is to: a) provide a coarse-filter spatial surrogate that broadly represents biodiversity patterns across the whole country; b) provide ecologically relevant environmental management units; and c) provide ecologically meaningful units that can be used in environmental planning and management (Dayaram et al. 2021). Consequently, it is generally regarded as the national map of terrestrial ecosystems for the country. While itself not formally mandated by law, in practice the National Vegetation Map is regarded as one of South Africa's foundational biodiversity datasets that has an important legislative function, as it informs a number of government environmental and biodiversity planning and management tools, such as maps of Critical Biodiversity Areas and Ecological Support Areas; protected area expansion strategies; and forms a basis for environmental impact assessment. Thus, poorly delineated vegetation types can lead to poor outcomes for conservation planning, land management and planning decisions, and ultimately the loss of biodiversity.

Each vegetation type delineates and describes the parts of the landscape that share similar plant communities that are influenced or determined by shared environmental drivers (Mucina & Rutherford 2006). These maps are essentially models of the natural variation observable in any landscape. They reduce the complexity and continuity of natural landscapes to a set of discrete categories. Irrespective of the methods used to classify landscapes there are invariably mapping errors, especially where the transition between ecosystems is a continuum rather than being marked by a clear boundary and where landscapes have been significantly modified. The National Vegetation Map aims to map the original or historical extent of ecosystems before contemporary settlements, croplands and mining modified landscapes. This is defined as the ecosystems present prior to the advent of permanent European settlement in South Africa circa 350 years ago (Mucina & Rutherford 2006). This is a pragmatic, albeit problematic, threshold as it does not consider the impact of pre-colonial populations on vegetation as significant, whereas it is highly likely that these populations did have extensive and significant impacts on ecosystems (e.g., Sadr 2022). As such, ecosystem classification and mapping can be particularly problematic in highly modified landscapes. In these instances, understanding the key environmental determinants of ecosystems is very important for mapping the original extent of vegetation.

Given the central role that the South African vegetation map plays in land and environmental management and biodiversity conservation, there is an imperative to maintain and update this map to reflect the best available data and emerging knowledge of historical vegetation. In the NW, concerns were raised during the preparation of the North West Biodiversity Sector Plan (NW READ 2015) that the current provincial vegetation map, which is based on the National Vegetation Map published in Mucina and Rutherford (2006), did not accurately reflect observed vegetation patterns. Three important accuracy issues were identified with respect to the 2006 vegetation map:

1. Inaccurate delineation of vegetation type boundaries.
2. Incorrect assignment of areas to a vegetation type class that did not reflect the characteristics of communities observed on the ground.
3. Redundant vegetation type descriptions and the existence of new or undescribed vegetation types.

Therefore, the purpose of this project was to resolve these issues in the NW vegetation map using currently available datasets, and to publish the revised vegetation map while aligning to SANBI's guidelines for revisions (Dayaram et al. 2021). Once published, the NW vegetation map can be reviewed for incorporation into the National Vegetation Map.

Whilst the current NW portion of the National Vegetation Map was published in 2006, the origin of the vegetation type boundaries as they currently appear in the map can be traced back to the agricultural land type maps prepared by the Department of Agriculture (Mucina et al. 2006). Land types were originally designed to serve the agricultural industry, and these would be areas with generally uniform climate, terrain and soil patterns (MacVicar et al. 1974).

The vegetation type boundaries as mapped in the 2006 National Vegetation Map are based on a vegetation map for the NW prepared by Bredenkamp and Brown (2003a). Unfortunately, all metadata relating to the development of this map was lost other than a hard-copy version of this map that was subsequently digitised[1]. The boundaries in this map, however, appear to be based predominately on the agricultural land type maps for NW. This assumption is supported by a comparison of the boundaries between the Bredenkamp and Brown (2003a) and the land type maps that indicates there is an 80% spatial coincidence of boundaries between the two maps (Figure 1). There has been significant development and refinement in the vegetation type concepts since Acocks (1953, 1975, 1988), but there has been comparatively little refinement of the vegetation type boundaries in the NW. Essentially, the majority of vegetation type boundaries as they appear in the 2006 vegetation map,

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[1] Leslie Brown and Ray Schaller pers. comm.

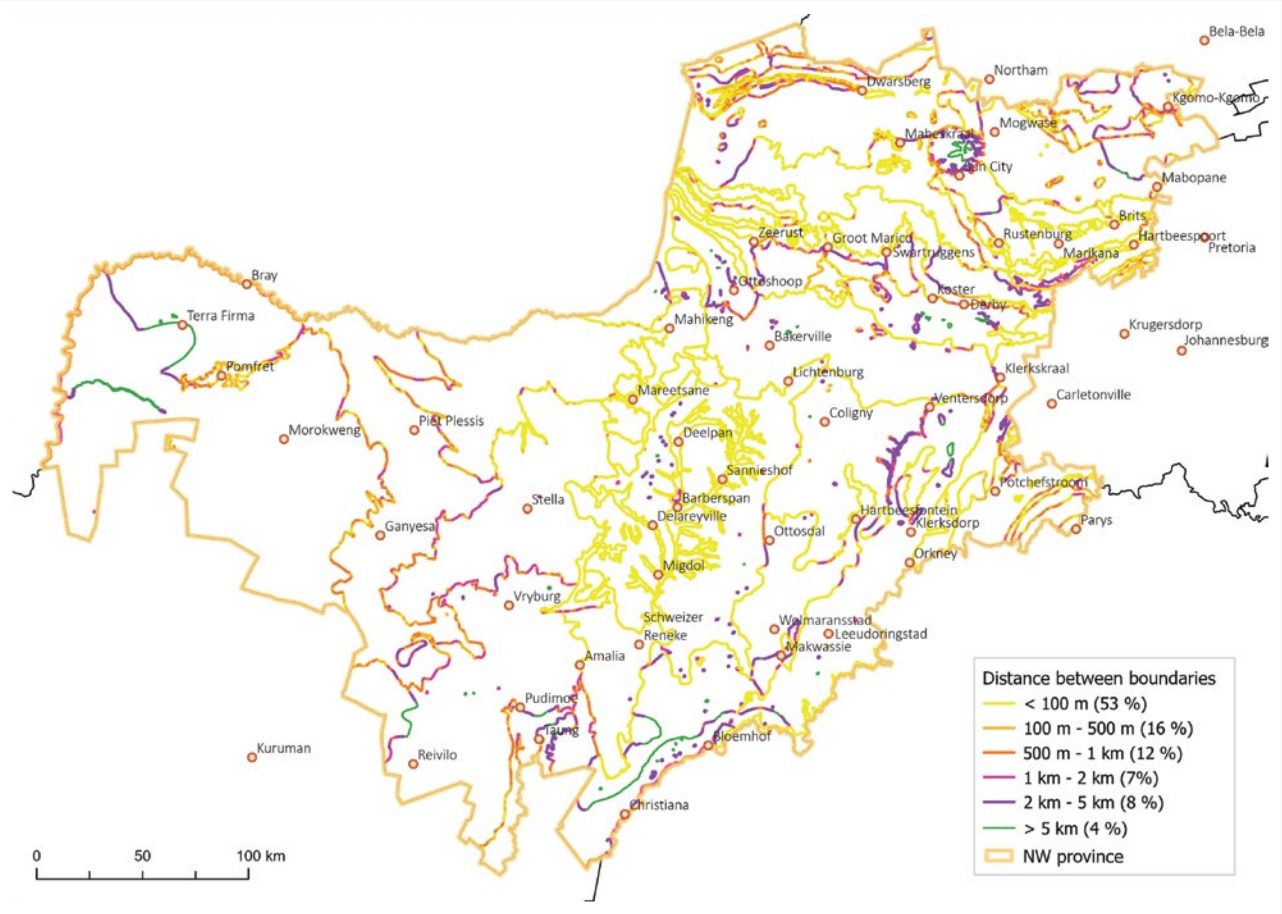

Figure 1. The spatial relationship between the vegetation type boundaries mapped in Bredenkamp and Brown (2003a) versus agricultural land types.

and subsequent 2018 map, were first mapped sometime in the 1980s. With the current availability of high-resolution aerial imagery, the emergence of desktop Geographic Information System (GIS) mapping technology, as well as the increased importance and use of the vegetation map for site-based environmental management, these have exposed the boundary errors inherent in the 2006 map and have highlighted the need to update the boundary mapping in this map.

The vegetation concepts and descriptions in the NW vegetation map draw on concepts in previous vegetation maps of South Africa (Acocks 1988; Low & Rebelo 1996), as well as the Bredenkamp and Brown (2003a) vegetation map. There are at least 93 published studies or reports relating directly to the vegetation of the NW. This body of literature, however, discusses almost exclusively vegetation concepts at the plant community scale. There are few quantitative studies that explicitly explore the floristic and environmental relationships between phytosociological units at the scale of the vegetation type, and none that attempt to define vegetation types using phytosociological approaches or discuss relationships between phytosociological units and vegetation types.

This is not unexpected as the bulk of the relevant vegetation science literature predates the current vegetation type concepts published in 2006. Post-2006 there has been very little phytosociological research published that covers the northwest region of South Africa. The absence of research directly exploring the relationships between phytosociological units and vegetation types, whilst not unexpected, highlights a very important vegetation science research gap. There is a clear need for more quantitative vegetation science research to develop and refine the current vegetation type concepts at the spatial scale at which they are conceived, as this provides the scientific justification for the concepts which is necessary to affirm the application of vegetation types in legislative and legal processes.

Bredenkamp and Brown (2003b) used a phytosociological approach to define higher-order vegetation association concepts for the Bankenveld in the Highveld region that are at a similar conceptual scale to vegetation types. Similarly, Winterbach (1998) and Winterbach et al. (2000) defined higher-order vegetation association concepts in the Arid Sweet Bushveld region of the NW to derive units that approach vegetation types. Van der Meulen and Westfall (1979) used agricultural land types as the basis to define and delineate vegetation units. In all these studies the same basic set of environmental elements are associated with these higher-order units,

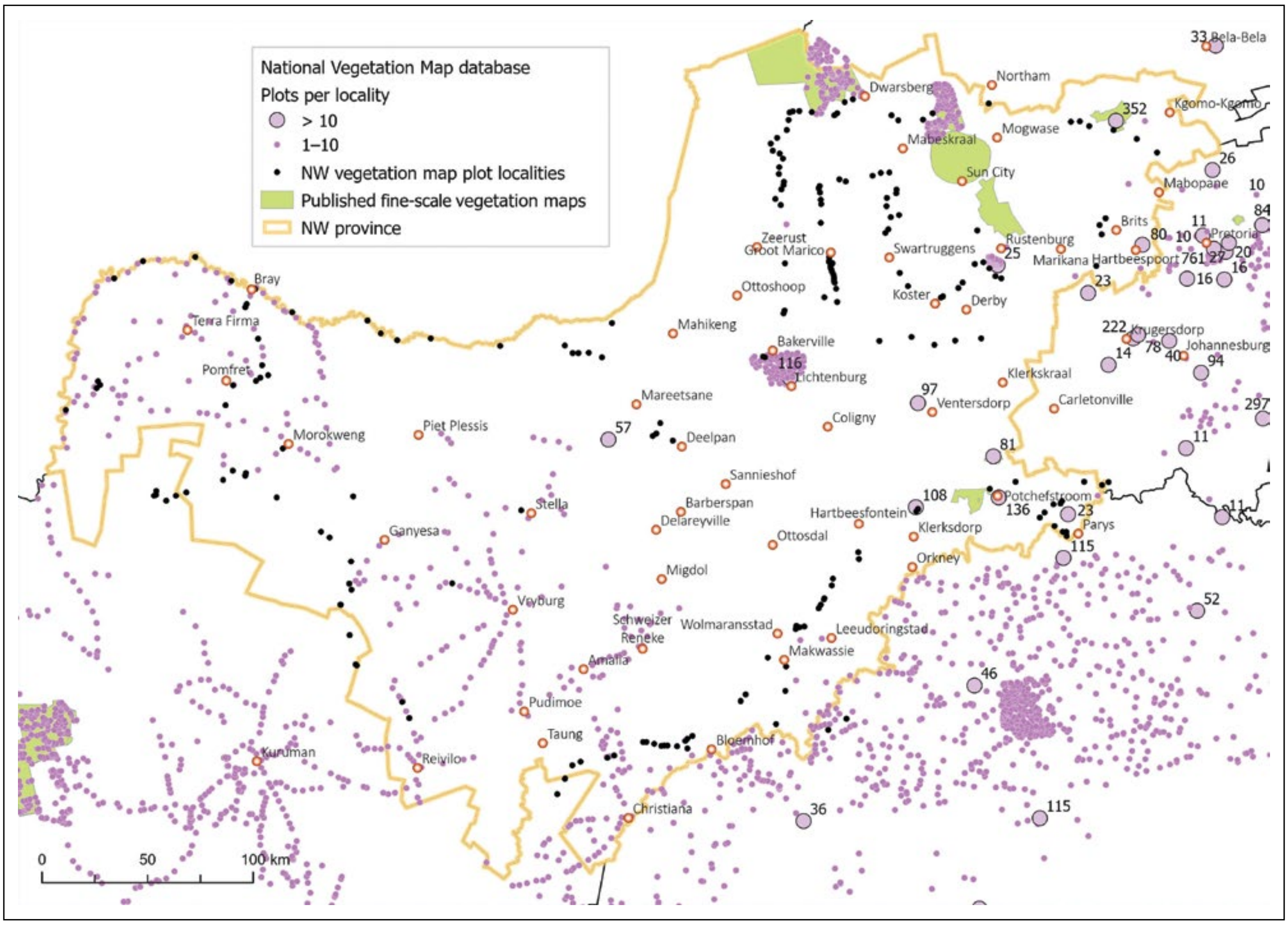

Figure 2. The extent of published fine-scale vegetation maps and available relevé data in and around the North West province (NW).

namely, soil (clay vs sandy soils on plains), terrain (plains vs mountains) and geology (quartzite vs igneous).

The spatial extent of individual vegetation studies relevant to the NW varies considerably. Some studies accept the agricultural land types as acceptable vegetation mapping units and conduct phytosociological analyses within these units (Bezuidenhout et al. 1993; Bezuidenhout et al. 1994a, 1994b) or across these units (Van der Meulen & Westfall 1979; Smit 2000). Other studies are conducted at a broader general geographic area (Morris 1976; Bredenkamp et al. 1989; Bezuidenhout & Bredenkamp 1990; Du Preez & Venter 1990a, 1990b; Bezuidenhout et al. 1994c, 1994d), or geological area (Bezuidenhout et al. 1988; Bezuidenhout et al. 1994b), or protected area (Van Zyl 1965; Coetzee 1975; Bredenkamp & Bezuidenhout 1990; Bredenkamp et al. 1994; Stalmans & De Wet 2003), or even part of a protected area (Brown & Bredenkamp 1994; Brown et al. 1995, 1996).

There are at least 29 published papers or reports that include fine-scale vegetation maps for their respective study areas that are relevant to the NW (Figure 2). Excluded from this list are phytosociological studies that used agricultural land types as the mapping unit rather than generating their own vegetation maps (e.g. Bezuidenhout et al. 1993; Bezuidenhout et al. 1994a, 1994b; Smit 2000; Van der Meulen & Westfall 1979). Collectively, these fine-scale maps cover 260 000 ha or 2.5% of the province. Despite there being a reasonable wealth of vegetation studies relevant to the region, there is a relative paucity in the extent of published vegetation maps. Added to this is the lack of curation of this information with none of the vegetation maps having spatial data in an accessible data archive.

Whilst the vegetation type concept has been accepted and used in South Africa at least since Acocks (1953), it was only in the 2006 version of the vegetation map that the current vegetation type concept was clearly articulated and defined (Mucina et al. 2006). Despite this major advance in the vegetation map, at least for the vegetation types occurring in the NW, it is not clear in the current delineation and description of the vegetation types what are the environmental variables or factors and species or communities that differentiate one vegetation type from another. These variables are implicit in the 'verbal models' used to define and delineate vegetation types (Mucina et al. 2006). However, a clear functional understanding or description of the differentiating factors between vegetation types is absent in the current descriptions of vegetation types. This is often cited by users of the NW vegetation map as being a limitation to using and interpreting the current map at the site level.

The National Vegetation Map is mapped at a broad spatial scale of a whole region or landscape. At the site level there will inevitably be boundary errors when using the vegetation map due to the difference between the scale of map production and scale of use. Therefore, users invariably have to interpret on-the-ground observations of vegetation patterns to 'fine scale' the vegetation map and determine the appropriate vegetation type or types occurring at a site. For users of the vegetation map to be able to make this interpretation at the site level, an understanding of the relationship between underlying environmental variables and the delineation of vegetation types is necessary. Having a clear understanding or model for where and why vegetation types occur is essential for the consistent and defensible mapping of vegetation boundaries, and ultimately the integrity of the vegetation type concept. Whilst this thinking is implicit in the current delineation of vegetation types, it is not, however, always made explicit or clear in the current vegetation type descriptions.

Given these observations and limitations of the current National Vegetation Map in the NW, the objectives of this project were to:

1. Draw on the existing vegetation type classification and descriptions to develop an identification key to vegetation types in the NW based on broad environmental variables.
2. Review existing studies, expert inputs and field observations to determine if there are redundant vegetation types (i.e., two vegetation types that can be merged) or undescribed vegetation types that need to be added to the map and, where possible, support proposed changes with numerical data, and use this information to update the current vegetation type descriptions.
3. Using the identification key in conjunction with available environmental spatial data and current high-resolution aerial imagery, remap vegetation type boundaries at a higher spatial resolution.

Study area

The NW is located on the African Plateau in central southern Africa on the border between South Africa and southern Botswana. The province is 104 881 km^2 and measures roughly 550 km (east–west) by 380 km (north–south). It straddles three major physiographic regions: in the west, parts of the Kalahari region, in the northeast, the Bushveld region and in the southeast, the Highveld region. These broad geographic regions are associated with three major drainage systems, namely the Molopo catchment in the Kalahari, Vaal catchment in the Highveld and Limpopo catchment in the Bushveld. The Molopo and Vaal systems drain towards the west into the Orange River and ultimately the Atlantic Ocean, whereas the Limpopo system drains to the northeast into the Indian Ocean (Figure 3A).

The median elevation of the NW is 1 271 m (mean 1 263 m, minimum 904 m, maximum 1 817 m). It is a relatively flat to gently undulating landscape punctuated with few and scattered regions of hills or mountains (Figure 3A). The major mountain ranges of the province are to be found in the Northern Bankenveld entailing the Dwarsberg and Rant van Tweedepoort, the Southern Bankenveld entailing the Magaliesberg, Witwatersberg, Enzelsberg and Swartruggens (Partridge et al. 2010), the Pilanesberg, the hilly landscape spanning between Wolmaransstad to Hartbeesfontein known as the Maquassi Hills, the predominantly east-facing low cliffs of the Ghaap Plateau forming a west dipping cuesta on the border between the NW and Northern Cape, and the Vredefort Dome in the southeast bordering Gauteng and Free State provinces. For all these mountain ranges the elevational range between the surrounding plains, valleys and summits rarely exceeds 300 m. The largest altitudinal gradient is located in the western Magaliesberg and Pilanesberg, where the maximum elevational range is approximately 600 m.

The climate of the NW is humid to semi-arid subtropical in character. Rainfall ranges from near 800 mm per annum in the Highveld on the eastern border with Gauteng and decreases to 250 mm in the extreme west of the province. There is a single summer-rainfall season from October through to April. Temperatures are coolest with higher incidence of frost on the Highveld, while the northern savannas are warmest. The Kalahari region has the warmest summer temperatures and the Bushveld region the mildest winters (Figure 4 and 5). Mucina and Rutherford (2006) described the climate of each vegetation type in more detail.

The geology of the region is varied (Figure 6); however, a singular dominant factor influencing vegetation patterns across the province is the widespread presence of Tertiary aeolian Kalahari sand. Outside of the Kalahari region, relic pockets of these sands can be encountered throughout most of the province. In terms of the underlying geology, important rock types with strong influences on vegetation are quartzite-rich sedimentary rocks giving rise to dystrophic sandy soils contrasted with mafic and ultramafic rocks giving rise to base-rich clay soils.

The flora of the NW is discussed in some detail by Hahn (2013). The flora is characterised by comprising mostly widespread species with very low levels of endemism. There are at least 2 786 species (2 387 indigenous and 399 not indigenous) recorded in the NW (see Supplementary Material 1) with 16 species (0.6%) known to be endemic or near-endemic to the province (Hahn 2013). Five species (44%) within this group of endemic species are associated with dystrophic quartzite geology of the Magaliesberg and Swartruggens regions, which is assigned to the Gold Reef Mountain Bushveld vegetation type (Table 1).

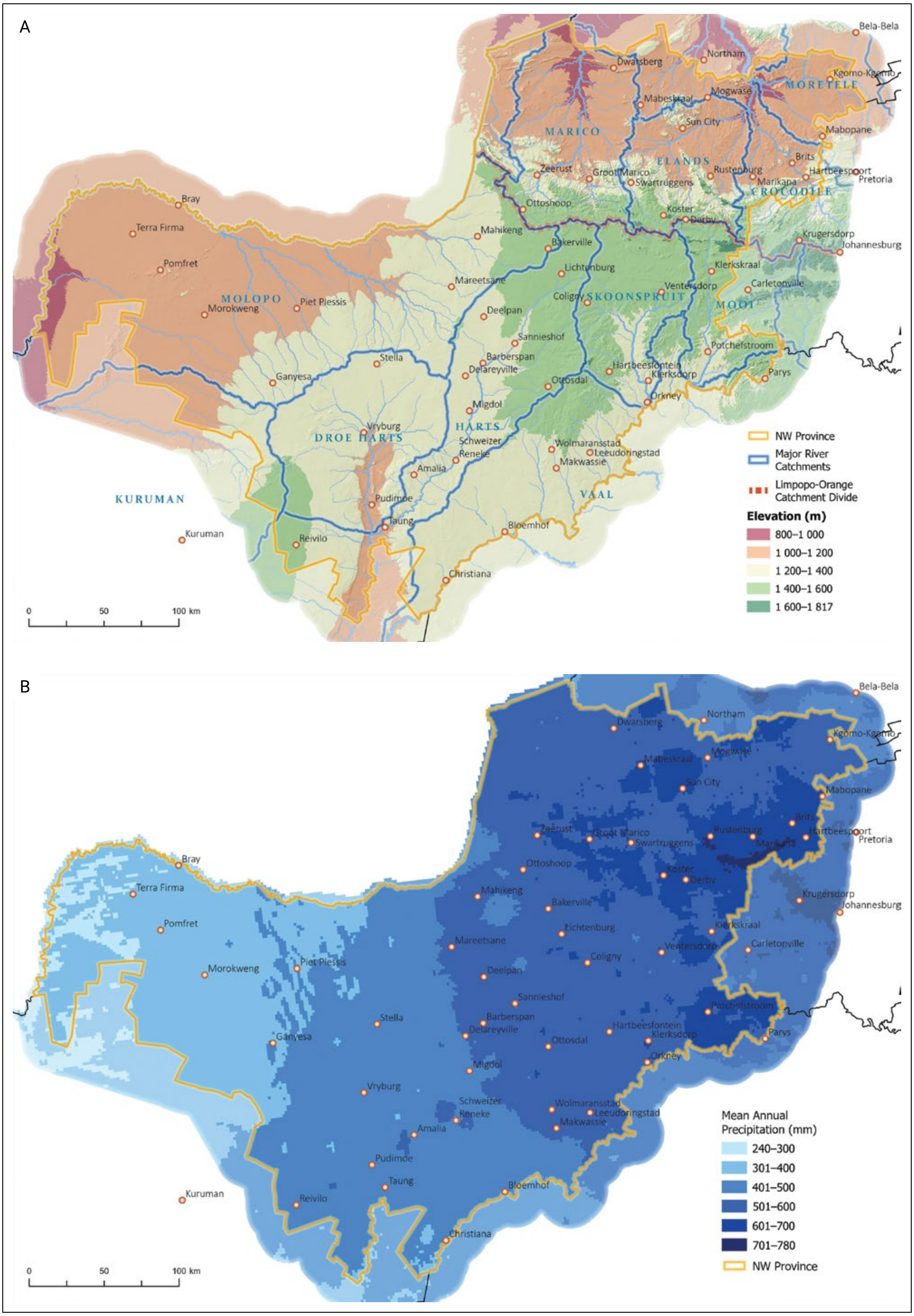

Figure 3. A, elevation and hydrology; B, mean annual precipitation in the North West province.

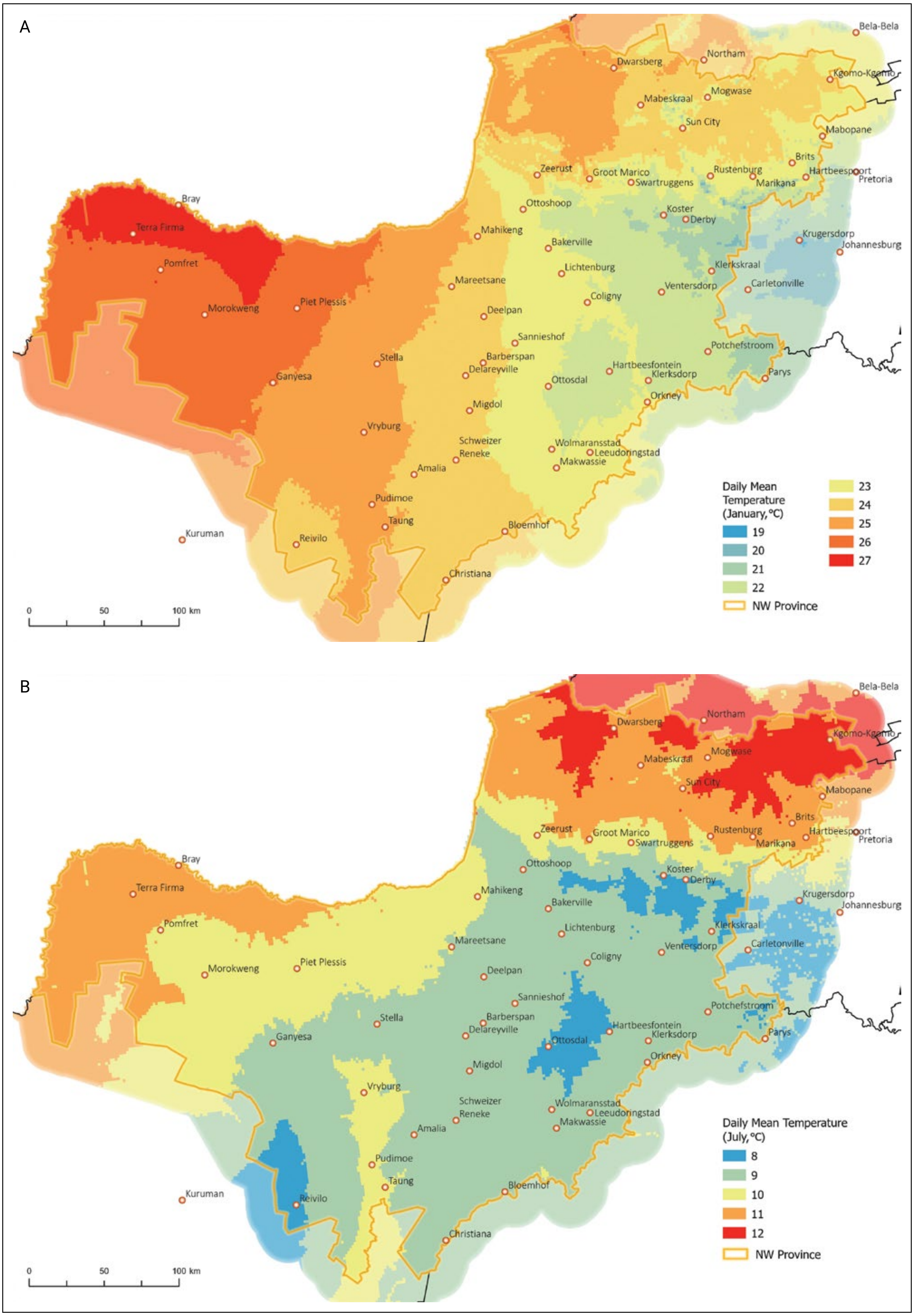

Figure 4. A, daily mean temperature for warmest; and B, coldest months in the North West province.

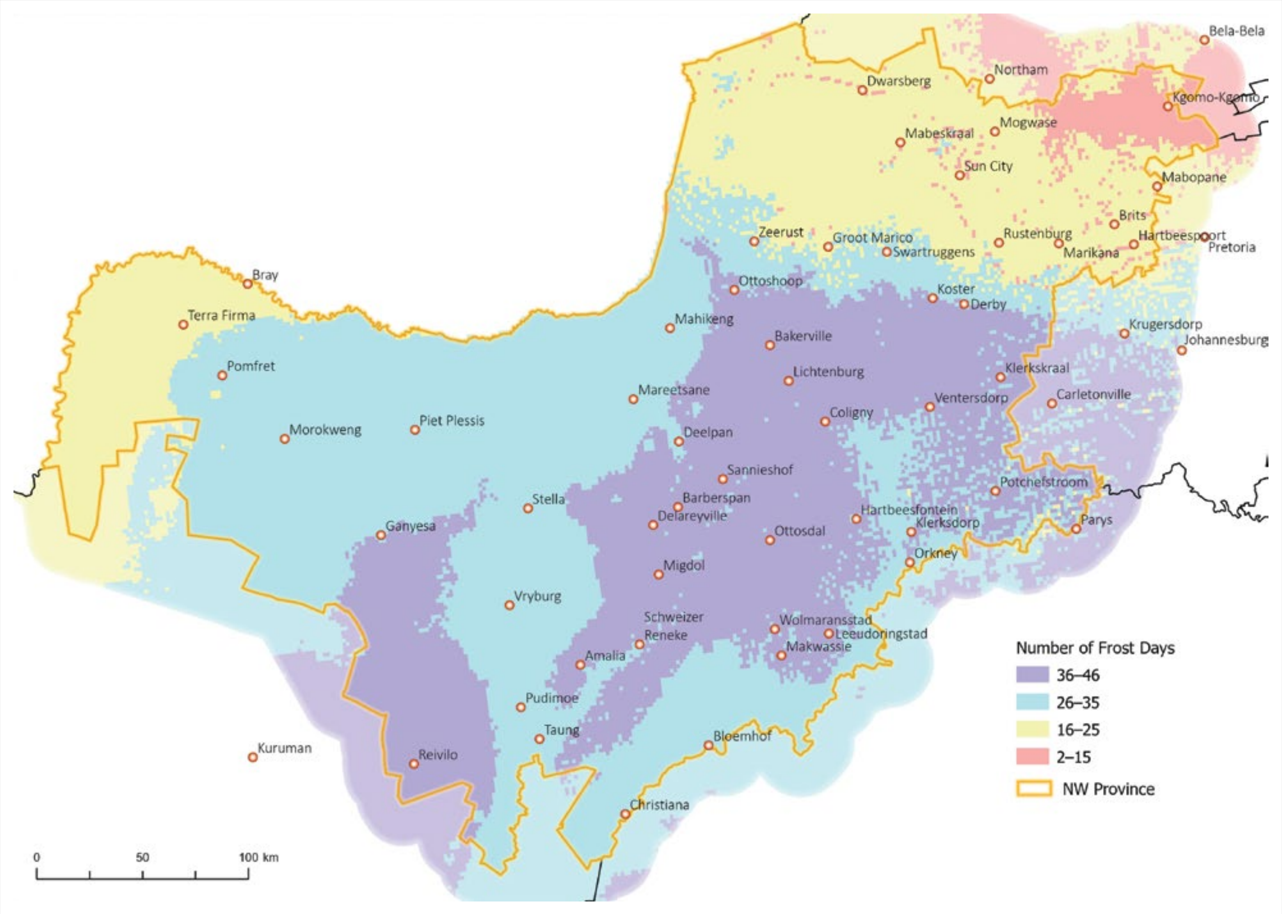

Figure 5. The number of frost days in the North West province.

Table 1. Known endemic (E) and near-endemic (nE) species to the North West province after Hahn (2013). Q = species endemic to the quartzite geology of the Gold Reef Mountain Bushveld vegetation type. R = Rare according to the national Red List categories

ID	Species name	Endemicity	Quartzite endemic
1	*Aloe peglerae*	nE	Q
2	*Blepharis angusta*	E	
3	*Brachystelma canum*	E, R	
4	*Brachystelma gracillimum*	E, R	Q
5	*Ceropegia insignis*	nE	
6	*Euphorbia knobelii*	E	Q
7	*Frithia pulchra*	nE	Q
8	*Gladiolus filiformis*	nE	
9	*Indigofera commixta*	E	
10	*Ledebouria atrobrunnea*	nE	
11	*Miraglossum laeve*	nE	
12	*Nuxia glomerulata*	nE	
13	*Pentzia stellata*	nE	
14	*Senecio holubii*	E, R	Q

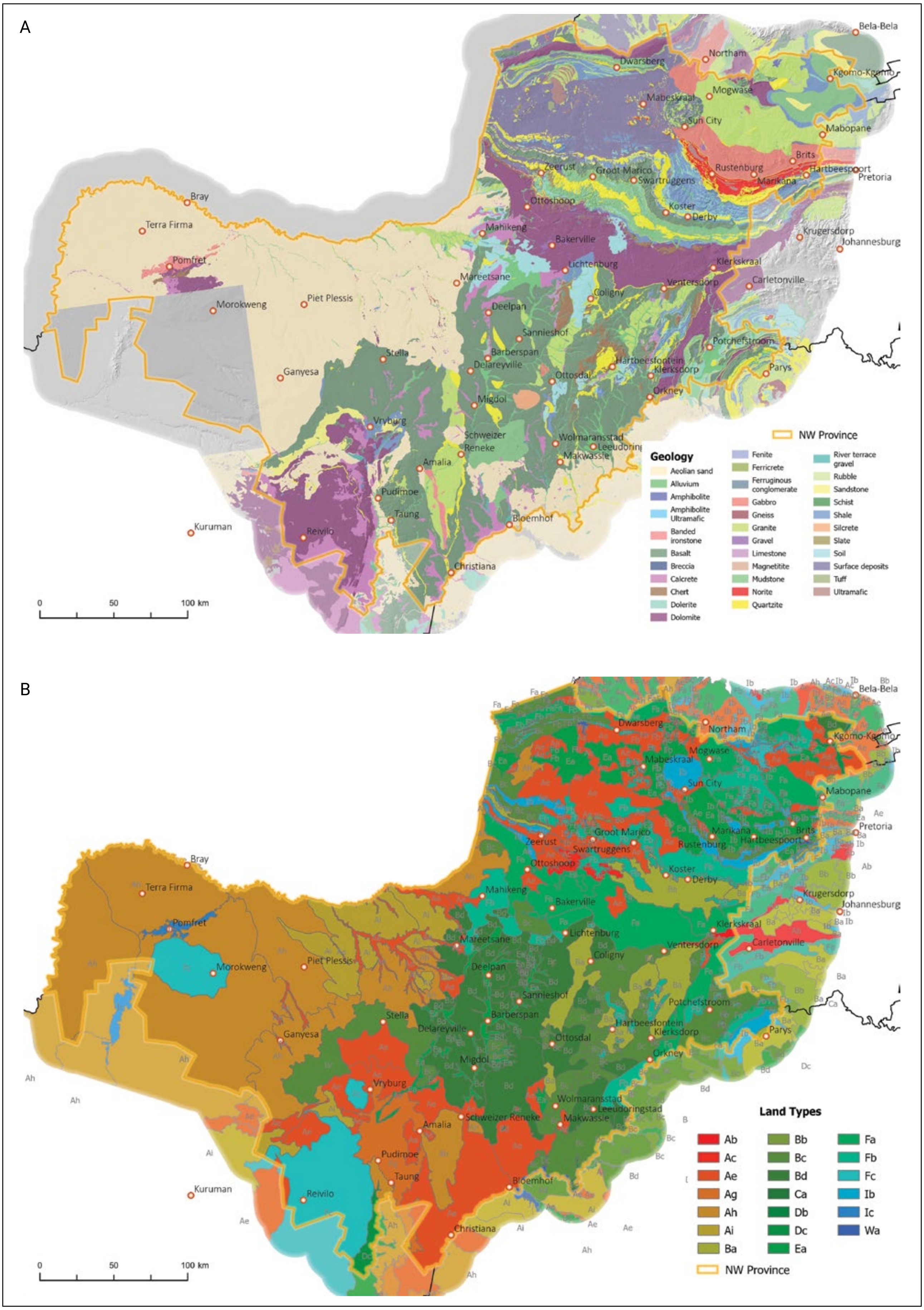

Figure 6. Spatial datasets used to inform the revision of the North West province vegetation map: A, simplified geology based on the 1:250 000 Geology of South Africa dataset; B, agricultural land types.

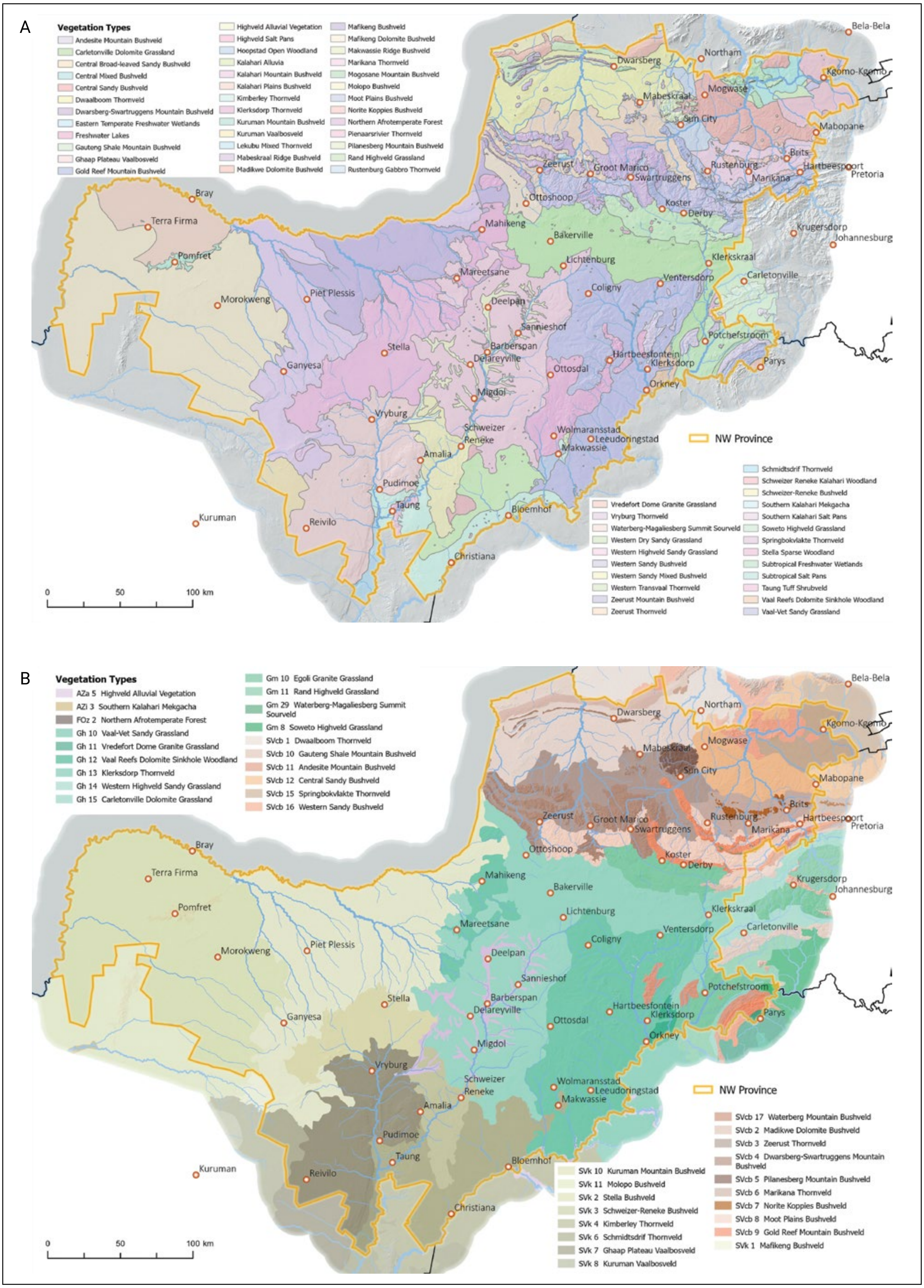

Figure 7. Spatial datasets used to inform the revision of the North West province vegetation map: A, Bredenkamp and Brown (2003a) vegetation map of the North West province; and B, the current 2018 National Vegetation Map (NVM) of South African vegetation types for the North West province (Dayaram et al. 2019).

Methods

Vegetation mapping

Vegetation type polygons were manually mapped using a heads-up digitising technique (Kennedy 2009). The vegetation types were delineated by interpreting patterns observed in colour aerial imagery overlayed with data layers representing the environmental variables used in the identification key to define vegetation types, namely: (1) land types as a proxy for soils, (2) simplified geology, and (3) terrain. In total 24 spatial datasets were used to inform the mapping process (Table 2).

In addition to the vegetation type identification key that provides a regional-scale framework for interpreting and mapping vegetation types, field observations and published descriptions of landform-vegetation relationships were also used to interpret patterns in aerial imagery at the local scale. Examples of landform–vegetation relationships include catena vegetation sequences or agricultural landtype map descriptions of landform–soil relationships. Different vegetation communities are associated with different landforms, and the landform–vegetation patterns tend to differ between vegetation types.

Vegetation identification key

To map vegetation in a logical and defensible manner it is necessary to have a framework for how vegetation types are classified and related to one another based on vegetation and floristic patterns and underlying environmental variables or determinants of vegetation types. Mucina et al. (2006) describe such a classification framework for how vegetation types in South Africa are circumscribed that forms the basis for how vegetation types are defined and mapped in the current National Vegetation Map. As described in the introduction, in the NW it is often not clear from the existing verbal models describing vegetation types what the defining features are of a vegetation type and what separates one vegetation type from another. Therefore, before any remapping of vegetation type boundaries could be attempted it was necessary to distil from existing vegetation type descriptions, expert inputs, published vegetation studies and field observations what the key environmental determinants are for each vegetation type, and use this information to develop an identification key to the vegetation types being mapped.

Vegetation type mapping is generally not concerned with mapping plant assemblage boundaries, but rather mapping higher-order spatial scale environmental discontinuities such as aspect, slope, elevation, soil, geology and landform. These are the same variables used to define land types, hence the close historic association between land types and vegetation types. The identification key developed here uses only broad environmental variables to define vegetation units stratified by bioregions or biomes, which represent the major climatic gradients present in the province.

As the first step in remapping the vegetation type boundaries of the NW, a basic identification key to the vegetation types of the province based on mappable environmental variables was developed. This key provided the quantitative framework within which input environmental and imagery datasets could be interpreted and vegetation boundaries mapped in the GIS. The key was based primarily on environmental attributes, but to increase utility for vegetation type identification in the field, broad vegetation structural attribute data was also included in the key. Vegetation structural characteristics are a function of underlying environmental attributes but are not always observable in single observation colour aerial imagery and therefore are not necessarily a reliable variable to use for mapping vegetation.

Species data

Plant species information was collated from existing data sources, as well as from data collected by this project. Data sources include:

1. Herbarium record data from SANBI's POSA database (SANBI 2016).
2. Published vegetation surveys that have been collated and archived in SANBI's National Vegetation Map Database (NVD).
3. Rapid vegetation survey plots and species observations conducted by this project and added to iNaturalist.

A current global species list for the province was created from herbarium record data. The purpose of the global species list was to provide a total flora context for the vegetation survey plot data and also provide a master species list against which to compare and correct plot species data. Data from SANBI's POSA database was obtained via a direct data request. The NW includes all or part of 229 unique quarter degree squares (QDS).

Vegetation survey plot data from most of the phytosociological studies that have been undertaken in the province have been collated and archived in the NVD. This is a national database that strives to archive all published vegetation survey data in South Africa. The database currently hosts data for about 58 000 plots. Plots from in and around the NW were extracted from this database for analysis. The purpose of this data was to: (1) inform the important species information in the vegetation type descriptions; and (2) to conduct an ordination analysis to compare the numerical

Table 2. Summary of the input datasets informing the mapping process

Original data source		Derived data layer name	Data format	Source
Digital Elevation Model (DEM)	1	Elevation (JAXA 30m DEM) (Figure 3A)	Raster	Japan Aerospace Exploration Agency (JAXA)
	2	Slope	Raster	This project using ArcGIS and Whitebox terrain analysis tools
	3	Aspect	Raster	
	4	Topographic position	Raster	
Geology	5	1:250 000 Geology of South Africa simplified to basic geological types (Figure 6A). Lithostratigraphic nomenclature of geological types are dispensed with in favour of simplified geological descriptions that link more closely with geology general physical and chemical properties.	Vector poly	Council for GeoScience Simplified types – this project
Modelled hydrology from DEM	6	Streamlines	Vector line	This project using Whitebox hydrological tools
	7	Catchments	Vector poly	
	8	Flow accumulation (indication of catena position)	Raster	
Hydrology	9	DWA Quinary Catchments	Vector poly	Department of Water and Sanitation (DWS)
	10	1:50 000 topographical map streamlines	Vector line	National Geo-spatial Information (NGI)
Wetland maps	11	National Wetland Atlas Map 6 Beta	Vector poly	South African National Biodiversity Institute (SANBI)
	12	Modelled depression wetlands of the Vaal subcatchment	Vector poly	SANBI
High-Resolution Aerial Imagery	13	ArcGIS Pro Online World Imagery	Raster	Environmental Systems Research Institute, Inc. (ESRI)
	14	Google Earth	Raster	Google Earth
	15	NGI RSA 2012 25 cm colour aerial	Raster	NGI
Vegetation maps	19	NW Bredenkamp and Brown 2003a (Figure 7A)	Vector poly	North West Department of Economic Development, Environment, Conservation and Tourism (NW DEDECT)
	20	National Vegetation Map 2018 (Figure 7B)	Vector poly	SANBI
	21	Agricultural land types (Figure 6B)	Vector poly	Department of Agriculture, Land Reform and Rural Development Agriculture Geographic Information System (AGIS)
Species data	22	National Vegetation Database of existing relevés (Figure 2)	Point	SANBI
	23	POSA quarter degree square (QDS) herbarium records	Polygon	SANBI
	24	Field survey plots and observations (iNat)	Point	This project

classification plot data versus the current classification of vegetation types.

The purpose of the rapid vegetation survey was to gather species and vegetation type (plant community and dominant species) observation data and photographs of vegetation types over as wide an area as possible in a limited time period. Field work was carried out over two growth seasons (2021/22 and 2022/23). The sampling method relied on noting discernible changes in the vegetation type along a catenal sequence then filling in a prescribed data sheet. A mobile version of the vegetation map was available on the CarryMap application for use in the field. This included both the 2018 version of the national map, as well as an unpublished NW vegetation map created by P. Desmet (NW READ 2015). This mobile app allowed for the live tracking of an individual as they move through the landscape and the identification of the existing mapped vegetation type present at a sampling location. Dominant species for a vegetation type were identified and noted and species with ethnobotanical importance, limited distribution or threatened and protected species were photographed and lodged on the iNaturalist App (https://www.inaturalist.org). Representative photographs of the vegetation type at each site were also uploaded with each species observation, and these were linked to the South African Vegetation Map project in iNaturalist.

Additional vegetation observation data from two previous field campaigns conducted by the authors in 2015 and 2018 were also collated and added to the observation database.

Expert data

Vegetation experts with experience of either mapping or using the provincial vegetation map were also engaged to canvas their opinion on what needed to be changed or updated in the revised map. Input from experts comprised either (1) verbal inputs, (2) relevé datasets that were not currently in the NVD or, (3) relevant documents or spatial data such as unpublished reports or GIS shapefiles that were not considered in Mucina and Rutherford (2006).

Results

Species data

In total 2 985 plots were extracted from the NVD that fall in or within 20 km of the NW (Figure 2). Of this 1 608 (54%) have no accurate georeference, i.e., locality information comprising a description only with no sample point latitude/longitude. For these plots, a geolocation was added based on the nearest town or area

Table 3. The most abundant species in North West province per growth form in the NVD plot data. Occurrence is expressed as percentage (%) presence in 2 985 plots analysed. Species names are abbreviated to species level only with no subspecific taxa considered in the analysis

Rank	Grass (Poaceae) species	%	Woody species	Family	%	Forb species	Family	%
1	*Aristida congesta*	54.3	*Grewia flava*	Malvaceae	27.0	*Felicia muricata*	Asteraceae	17.6
2	*Themeda triandra*	48.2	*Ziziphus mucronata*	Rhamnaceae	24.6	*Commelina africana*	Commelinaceae	15.1
3	*Heteropogon contortus*	33.0	*Dichrostachys cinerea*	Fabaceae	18.9	*Senecio venosus*	Asteraceae	14.1
4	*Digitaria eriantha*	32.1	*Vachellia karroo*	Fabaceae	18.2	*Dicoma anomala*	Asteraceae	13.7
5	*Brachiaria serrata*	28.3	*Vachellia tortilis*	Fabaceae	17.6	*Anthospermum rigidum*	Rubiaceae	13.3
6	*Eragrostis curvula*	27.9	*Diospyros lycioides*	Ebenaceae	13.4	*Hilliardiella oligocephala*	Asteraceae	13.2
7	*Eragrostis lehmanniana*	26.8	*Elephantorrhiza elephantina*	Fabaceae	13.0	*Schkuhria pinnata*	Asteraceae	12.8
8	*Elionurus muticus*	26.5	*Ehretia rigida*	Boraginaceae	11.2	*Barleria macrostegia*	Acanthaceae	12.6
9	*Setaria sphacelata*	26.0	*Senegalia caffra*	Fabaceae	10.9	*Asparagus laricinus*	Asparagaceae	11.8
10	*Melinis repens*	24.0	*Vachellia erioloba*	Fabaceae	10.9	*Pollichia campestris*	Caryophyllaceae	11.5

Table 3. The most abundant species in North West province per growth form in the NVD plot data. Occurrence is expressed as percentage (%) presence in 2 985 plots analysed. Species names are abbreviated to species level only with no subspecific taxa considered in the analysis (continued)

Rank	Grass (Poaceae) species	%	Woody species	Family	%	Forb species	Family	%
11	*Cynodon dactylon*	23.4	*Searsia leptodictya*	Anacardiaceae	10.8	*Asparagus suaveolens*	Asparagaceae	11.4
12	*Cymbopogon pospischilii*	23.1	*Gymnosporia heterophylla*	Celastraceae	10.8	*Crabbea angustifolia*	Acanthaceae	11.2
13	*Diheteropogon amplectens*	21.9	*Senegalia mellifera*	Fabaceae	10.7	*Kyphocarpa angustifolia*	Amaranthaceae	10.8
14	*Eragrostis rigidior*	19.5	*Tarchonanthus camphoratus*	Asteraceae	10.0	*Asparagus africanus*	Asparagaceae	10.7
15	*Pogonarthria squarrosa*	18.0	*Searsia lancea*	Anacardiaceae	9.4	*Justicia anagalloides*	Acanthaceae	10.3
16	*Schmidtia pappophoroides*	17.9	*Vachellia hebeclada*	Fabaceae	8.6	*Gazania krebsiana*	Asteraceae	9.1
17	*Eragrostis racemosa*	17.5	*Ziziphus zeyheriana*	Rhamnaceae	8.6	*Solanum campylacanthum*	Solanaceae	9.0
18	*Trachypogon spicatus*	17.4	*Searsia pyroides*	Anacardiaceae	8.1	*Indigofera daleoides*	Fabaceae	8.8
19	*Schizachyrium sanguineum*	16.1	*Combretum molle*	Combretaceae	8.0	*Monsonia angustifolia*	Geraniaceae	8.5
20	*Panicum maximum*	15.3	*Terminalia sericea*	Combretaceae	7.6	*Hermannia depressa*	Malvaceae	8.4
21	*Stipagrostis uniplumis*	14.7	*Dombeya rotundifolia*	Malvaceae	7.4	*Cyanotis speciosa*	Commelinaceae	8.3
22	*Melinis nerviglumis*	14.4	*Combretum apiculatum*	Combretaceae	7.1	*Hermannia tomentosa*	Malvaceae	8.3
23	*Eragrostis superba*	14.2	*Vachellia nilotica*	Fabaceae	6.2	*Lippia scaberrima*	Verbenaceae	8.3
24	*Cymbopogon caesius*	14.0	*Euclea undulata*	Ebenaceae	5.9	*Chamaecrista mimosoides*	Fabaceae	8.2
25	*Eustachys paspaloides*	13.8	*Combretum zeyheri*	Combretaceae	5.7	*Indigofera comosa*	Fabaceae	8.0
26	*Aristida stipitata*	13.2	*Vangueria infausta*	Rubiaceae	5.5	*Nidorella hottentotica*	Asteraceae	8.0
27	*Andropogon schirensis*	12.9	*Euclea crispa*	Ebenaceae	5.3	*Hibiscus pusillus*	Malvaceae	7.7
28	*Triraphis andropogonoides*	12.6	*Zanthoxylum capense*	Rutaceae	5.2	*Waltheria indica*	Malvaceae	7.7
29	*Tragus berteronianus*	12.5	*Protea caffra*	Proteaceae	5.0	*Kohautia amatymbica*	Rubiaceae	7.4
30	*Loudetia simplex*	12.0	*Pappea capensis*	Sapindaceae	5.0	*Limeum viscosum*	Limeaceae	7.4

that could be determined from the plot locality description data, or failing this, locality clues present in the title of the project or source publication. The sampling density of plots is low. For the 2 985 plots selected from the NW plus 20 km buffer, this is a sampling density of approximately 1 plot per 50 km^2; however, only 785 plots fall within the NW equating to a sampling density of approximately 1 plot per 130 km^2.

In total the NVD dataset contains 28 705 records for 1 610 species (Table 3). This equates to a sampling density of approximately 1 record per 5 km^2. Note that only genus and species are considered here and no subspecific taxa are considered. In contrast to the vegetation survey plot data, the global species list, derived from POSA herbarium record data for the province at the genus and species levels, contains 3 040 taxa of which 407 are not native (Table 4). That means for indigenous species (2 633 taxa) only 61% of species known to occur in the province have been recorded in nearly 3 000 vegetation survey plots.

Vegetation type identification key

An identification key for the vegetation types of the NW (Table 6) was developed based on 15 broad environmental variables grouped into five variable categories (Table 5). The identification key is able to discriminate and identify all 36 terrestrial vegetations types that occur in the province plus the three 'azonal' types associated with hydrologically driven ecosystems.

Summary of changes made to the vegetation map

Changes to the NW vegetation map are summarised according to the potential types of changes described by the National Vegetation Map Committee (Table 7). The changes in vegetation type extents are summarised in Table 8.

Table 4. The 100 most widespread indigenous plant species in North West province as recorded in the POSA herbarium dataset. QDS = the number of unique quarter degree squares in the North West province in which a species is recorded (total QDS in NW = 229)

	Species name	Family	QDS		Species name	Family	QDS		Species name	Family	QDS
1	*Aristida congesta*	Poaceae	103	35	*Aptosimum elongatum*	Scrophulariaceae	51	69	*Gymnosporia buxifolia*	Celastraceae	40
2	*Eragrostis curvula*	Poaceae	94	36	*Ozoroa paniculosa*	Anacardiaceae	51	70	*Indigofera daleoides*	Fabaceae	40
3	*Commelina africana*	Commelinaceae	93	37	*Ziziphus mucronata*	Rhamnaceae	51	71	*Panicum maximum*	Poaceae	40
4	*Digitaria eriantha*	Poaceae	92	38	*Helichrysum nudifolium*	Asteraceae	50	72	*Pavetta zeyheri*	Rubiaceae	40
5	*Aristida stipitata*	Poaceae	78	39	*Solanum campylacanthum*	Solanaceae	49	73	*Pavonia burchellii*	Malvaceae	40
6	*Stipagrostis uniplumis*	Poaceae	75	40	*Vahlia capensis*	Vahliaceae	49	74	*Wahlenbergia undulata*	Campanulaceae	40
7	*Melinis repens*	Poaceae	74	41	*Pollichia campestris*	Caryophyllaceae	48	75	*Cyperus decurvatus*	Cyperaceae	39
8	*Searsia pyroides*	Anacardiaceae	74	42	*Barleria macrostegia*	Acanthaceae	47	76	*Eragrostis rigidior*	Poaceae	39
9	*Diospyros lycioides*	Ebenaceae	71	43	*Hermbstaedtia odorata*	Amaranthaceae	47	77	*Hibiscus pusillus*	Malvaceae	39
10	*Grewia flava*	Malvaceae	70	44	*Lantana rugosa*	Verbenaceae	47	78	*Polygala hottentotta*	Polygalaceae	39
11	*Themeda triandra*	Poaceae	65	45	*Senna italica*	Fabaceae	47	79	*Trichoneura grandiglumis*	Poaceae	39

Table 4. The 100 most widespread indigenous plant species in North West Province as recorded in the POSA herbarium dataset. QDS = the number of unique quarter degree squares in the North West province in which a species is recorded (total QDS in NW = 229) (continued)

	Species name	Family	QDS		Species name	Family	QDS		Species name	Family	QDS
12	*Dicoma anomala*	Asteraceae	64	46	*Commelina livingstonii*	Commelinaceae	46	80	*Eustachys paspaloides*	Poaceae	38
13	*Rhynchosia totta*	Fabaceae	62	47	*Monsonia angustifolia*	Geraniaceae	46	81	*Helichrysum argyrosphaerum*	Asteraceae	38
14	*Cymbopogon pospischilii*	Poaceae	61	48	*Ziziphus zeyheriana*	Rhamnaceae	46	82	*Phyllanthus parvulus*	Phyllanthaceae	38
15	*Eragrostis lehmanniana*	Poaceae	61	49	*Cymbopogon caesius*	Poaceae	45	83	*Croton gratissimus*	Euphorbiaceae	37
16	*Eragrostis superba*	Poaceae	61	50	*Eragrostis gummiflua*	Poaceae	45	84	*Cyphocarpa angustifolia*	Amaranthaceae	37
17	*Felicia muricata*	Asteraceae	61	51	*Nidorella resedifolia*	Asteraceae	45	85	*Limeum viscosum*	Limeaceae	37
18	*Setaria sphacelata*	Poaceae	59	52	*Tragus berteronianus*	Poaceae	45	86	*Schoenoplectus muricinux*	Cyperaceae	37
19	*Schmidtia pappophoroides*	Poaceae	58	53	*Corchorus asplenifolius*	Malvaceae	44	87	*Aristida adscensionis*	Poaceae	36
20	*Sporobolus fimbriatus*	Poaceae	58	54	*Eragrostis chloromelas*	Poaceae	44	88	*Elephantorrhiza elephantina*	Fabaceae	36
21	*Vachellia karroo*	Fabaceae	57	55	*Hilliardiella elaeagnoides*	Asteraceae	44	89	*Eragrostis pallens*	Poaceae	36
22	*Eragrostis trichophora*	Poaceae	56	56	*Sphedamnocarpus pruriens*	Malpighiaceae	44	90	*Ipomoea bolusiana*	Convolvulaceae	36
23	*Pogonarthria squarrosa*	Poaceae	56	57	*Tarchonanthus camphoratus*	Asteraceae	44	91	*Scabiosa columbaria*	Dipsacaceae	36
24	*Bulbostylis burchellii*	Cyperaceae	55	58	*Lippia scaberrima*	Verbenaceae	43	92	*Sida chrysantha*	Malvaceae	36
25	*Enneapogon scoparius*	Poaceae	55	59	*Elionurus muticus*	Poaceae	42	93	*Triraphis andropogonoides*	Poaceae	36
26	*Geigeria burkei*	Asteraceae	54	60	*Gazania krebsiana*	Asteraceae	42	94	*Chlorophytum fasciculatum*	Agavaceae	35
27	*Heteropogon contortus*	Poaceae	54	61	*Gomphocarpus fruticosus*	Apocynaceae	42	95	*Olea europaea*	Oleaceae	35
28	*Panicum coloratum*	Poaceae	54	62	*Ipomoea obscura*	Convolvulaceae	42	96	*Salvia runcinata*	Lamiaceae	35
29	*Anthephora pubescens*	Poaceae	53	63	*Searsia leptodictya*	Anacardiaceae	42	97	*Schizachyrium sanguineum*	Poaceae	35
30	*Cynodon dactylon*	Poaceae	53	64	*Teucrium trifidum*	Lamiaceae	42	98	*Terminalia sericea*	Combretaceae	35
31	*Cyperus margaritaceus*	Cyperaceae	53	65	*Xenostegia tridentata*	Convolvulaceae	42	99	*Asparagus suaveolens*	Asparagaceae	34
32	*Aerva leucura*	Amaranthaceae	52	66	*Fingerhuthia africana*	Poaceae	41	100	*Chamaecrista biensis*	Fabaceae	34
33	*Brachiaria nigropedata*	Poaceae	52	67	*Hermannia tomentosa*	Malvaceae	41				
34	*Anthospermum rigidum*	Rubiaceae	51	68	*Mundulea sericea*	Fabaceae	41				

Table 5. Summary of the environmental variables used to construct the identification key in Table 6 used to define and map vegetation types

Hierarchical order of variable	Variable category	Variable name
1	Flooding	(a) alluvial (b) terrestrial
2	Bioregion	(a) Bushveld (b) Kalahari (c) Highveld
3	Terrain	(a) plains (b) mountainous/rocky habitats (including pediments)
4	Geology	(a) aeolian (b) quartzite and sandstone (c) shale and mudstone (d) dolomite (e) igneous mafic (f) igneous felsic
5	Soil	(a) sand (b) clay

Table 6. An identification key to the vegetation types of the North West province based on broad environmental and vegetation structure characteristics

Key level	Environmental variable		Vegetation type
1	Alluvial Vegetation *Vegetation types where the occasional presence of surface water is a primary determinant of the vegetation type, such as valley bottoms, alluvial, wetland or occasionally flooded. Also referred to as azonal vegetation types.*		
1.1	North: Central Bushveld Bioregion	1	Subtropical Alluvial Vegetation
1.2	West: Eastern Kalahari Bioregion	2	Southern Kalahari Mekgacha
1.3	South: Grassland Bioregion	3	Highveld Alluvial Vegetation
2	Terrestrial Vegetation		
2.1	North: Central Bushveld Bioregion		
2.1.1	Mountains and koppies		
2.1.1.1	Shale and mudstone	4	Dwarsberg-Swartruggens Mountain Bushveld
2.1.1.2	Dolomite	5	Madikwe Dolomite Bushveld
2.1.1.3	Norite/gabbro (mafic)	6	Norite Koppies Bushveld
2.1.1.4	Pilanesberg	7	Pilanesberg Mountain Bushveld
2.1.1.5	Quartzite and sandstone	8	Waterberg Mountain Bushveld
2.1.1.6	Granite (felsic)	9	Central Sandy Mountain Bushveld
2.1.2	Plains		
2.1.2.1	Heavy clay (vertisols)		
2.1.2.1.1	West	10	Dwaalboom Thornveld
2.1.2.1.2	Swartruggens (clay soils)	11	Zeerust Thornveld
2.1.2.1.3	Central/Rustenburg	12	Marikana Thornveld
2.1.2.1.4	East/Springbokvlakte	13	Springbokvlakte Thornveld
2.1.2.2	Sand		

Table 6. An identification key to the vegetation types of the North West province based on broad environmental and vegetation structure characteristics (continued)

Key level	Environmental variable		Vegetation type
2.1.2.2.1	Aeolian/Kalahari sand		
2.1.2.2.1.1	West of Crocodile River/Pilanesberg	14	Western Sandy Bushveld
2.1.2.2.1.2	East of Crocodile River/Pilanesberg (more mixed veld broadleaf and acacia)	15	Western Sandy Bushveld (East)
2.1.2.2.2	Fersiallitic soils (medium sandy clay loams with good drainage, derived from mafic (basic) rocks)/undulating landscapes with pronounced catenas	16	Central Sandy Bushveld
2.1.2.2.3	Silica rich sand in valleys derived from quartzite hills (and sometimes Kalahari sand), valleys of the Magaliesberg	17	Moot Plains Bushveld
2.2	West: Eastern Kalahari Bioregion		
2.2.1	Mountains and koppies	18	Kuruman Mountain Bushveld
2.2.2	Plains		
2.2.2.1	Calcrete or dolomite		
2.2.2.1.1	Thornveld	19	Morokweng Thornveld
2.2.2.2.2	Bushveld	20	Ghaap Plateau Vaalbosveld
2.2.2.2	Deep sand over calcrete		
2.2.2.2.1	East	21	Stella Bushveld
2.2.2.2.2	West	22	Kuruman Vaalbosveld
2.2.2.3	Deep sand over dorbank		
2.2.2.3.1	Sand eroding, dorbank and calcrete (along streams) exposed	23	Vryburg Thornveld
2.2.2.3.2	Deep sand (mixed), Molopo catchment	24	Mafikeng Bushveld
2.2.2.3.2	Deep sand (mixed), east of Harts River	25	Schweizer-Reneke Bushveld
2.2.2.3.4	Deeper sand (red)	26	Molopo Bushveld
2.2.2.4	Deep alluvial soils, no occasional flooding	27	Schmidtsdrif Thornveld
2.3	South: Grassland Bioregion		
2.3.1	Mountains and koppies		
2.3.1.2	Quartzite		
2.3.1.2.1		29	Gold Reef Mountain Bushveld
2.3.1.2.2	Montane above 1600 m/pockets of deep sandy soils	30	Waterberg-Magaliesberg Summit Sourveld
2.3.1.3	Shale and mudstone	31	Gauteng Shale Mountain Bushveld
2.3.1.4	Igneous (basalt: dolerite, andesite, etc.)	32	Andesite Mountain Bushveld
2.3.1.5	Granite (includes koppies and plains)	33	Vredefort Dome Granite Grassland
2.3.2	Plains		
2.3.2.1	Sandy soils		
2.3.2.1.1	Potchefstroom eastwards (soil clay content > 20%, depth > 0.5 m) tall grassland > 0.5 m, average annual rainfall > 600 mm	34	Rand Highveld Grassland
2.3.2.1.2	Central (soil clay content < 20%, depth > 0.5 m) tall grassland >0.5 m, average annual rainfall < 600 mm	35	Vaal-Vet Sandy Grassland

Table 6. An identification key to the vegetation types of the North West province based on broad environmental and vegetation structure characteristics (continued)

Key level	Environmental variable		Vegetation type
2.3.2.1.3	West (soil clay content < 25%, depth < 0.5 m) short grassland < 0.5 m often with calcrete in the landscape, average annual rainfall < 600 mm	36	Western Highveld Sandy Grassland
2.3.2.2	Dolomite		
2.3.2.2.1	Mostly grassland	37	Carletonville Dolomite Grassland
2.3.2.2.2	Prominent woody element present, sinkholes filled with Aeolian sand (dolines)	38	Vaal Reefs Dolomite Sinkhole Woodland
2.3.2.3	Clay, undulating landscapes with shallow stony soils derived from igneous, sedimentary or metamorphic rocks		
2.3.2.3.1	West of Bloemhof (*Vachellia tortilis*), average annual rainfall < 500 mm, < 35 frost days per annum	39	Kimberley Thornveld
2.3.2.3.2	East of Bloemhof (*Vachellia caffra* and *V. karroo*), average annual rainfall > 500 mm, > 35 frost days per annum	40	Klerksdorp Thornveld
2.4	Evergreen forest	41	Northern Afrotemperate Forest

Table 7. Summary of the changes made to the North West province vegetation map. Changes are summarised according to the potential type of changes described in the South African National Ecosystem Classification System Handbook* (SANBI 2023)

No.	Types of change
	Minor change
MN1	**Boundary shifts (realignment)** All vegetation type boundaries have been remapped from scratch. See text for rational behind updating boundary mapping. As the current map is based on a map first developed in the 1980s, it is inevitable that most boundaries will change given the better mapping tools and resolution of spatial data available for mapping. Remapping of boundaries does not imply that the original land type map or concept is wrong, just that the boundaries are inaccurate.
MN2	**Creation of a subtype/community within an existing vegetation type** Within FOz 2 **Northern Afrotemperate Forest** a new subvegetation type, **Olea Sclerophyllous Forest**, is discussed but not proposed as a recognised unit as yet. This forest unit is widespread in eastern southern Africa within other vegetation types typically on slopes where fire is excluded.
MN3	**Change in vegetation type name (without spatial or description changes).** *Special circumstances for this change are described in the handbook. Not applicable.
MN4	**Change in vegetation type description, e.g., list of endemic species** All vegetation type descriptions have been updated based on: (1) Mucina and Rutherford (2006) vegetation map description. (2) Bredenkamp and Brown (2003a) vegetation map descriptions. (3) Field observations. (4) Species information in the NVD relevé database. (5) Vegetation accounts in relevant scientific papers, theses and reports. (6) Inputs from expert stakeholders. Endemic species have not been re-assessed. Refer to Hahn (2013) for a detailed analysis and description of species endemic to the NW.
MN5	**Boundary shifts when neighbouring country or coastal borders are redefined** Not applicable.

Table 7. Summary of the changes made to the North West province vegetation map. Changes are summarised according to the potential type of changes described in the South African National Ecosystem Classification System Handbook* (SANBI 2023) (continued)

No.	Types of change
MN6	**The creation of new polygons of an existing vegetation type that may be disjunct from existing polygons of that type and beyond a reasonable* range extension or reduction.** *To be determined by the National Vegetation Map Committee on a case-by-case basis. Two existing vegetation types are included in the province that were previously not mapped as occurring in the province, namely, **Subtropical Alluvial Vegetation** and **Waterberg Mountain Bushveld**. The current map does not have any alluvial vegetation category in the Bushveld region. Given the presence of several large rivers, as well as extensive floodplain ecosystems it is necessary to bring **Subtropical Alluvial Vegetation** into the province to accommodate these ecosystems. This alluvial ecosystem type is not indicated as occurring in the province in the 2018 version of the National Vegetation Map, however, it should be noted that this type was present in the 2006 version of the National Vegetation Map to accommodate the Kgomo Kgomo floodplain along the Moretele River. **Waterberg Mountain Bushveld** occurs just north of the province. Mountain bushveld vegetation on quartzite along the northern border of the province should be assigned to this vegetation unit as these mountains are contiguous with the Waterberg Mountain complex (Partridge et al. 2010), and while the mountain bushveld vegetation is similar to that of the northern Bankenveld in terms of structure and species, the mountains are geographically separate.
	Major change
MJ1	**Removal of a vegetation type from the classification system or downgrading a type to a level below a vegetation type, e.g., subtypes.** Not applicable.
MJ2	**Create new vegetation type (replace existing) or upgrading of a subtype to a type.** Three new vegetation types are proposed namely, **Vryburg Thornveld, Morokweng Thornveld** and **Central Sandy Mountain Bushveld**. These are not new vegetation concepts. All three types have been recognised and mapped by previous authors; however, these units were (erroneously) lumped with other vegetation types with the creation of the 2006 National Vegetation Map. Both **Vryburg Thornveld** and **Morokweng Thornveld** exist as units in the land type map and are recognised as distinct phytosociological units by Smit (2000), namely, *Acacia erioloba – Acanthosicyos naudinianus – Dichrostachys cinerea* vlaktes (plains) and *Acacia mellifera – Acacia hebeclada – Heliotropium ciliatum* sandvlaktes (sandplains), respectively. In Bredenkamp and Brown (2003a) **Vryburg Thornveld** is retained as unit but not **Morokweng Thornveld**, however, in Mucina and Rutherford (2006) both units are lost. **Morokweng Thornveld** (Figure 8) is associated with a karst landscape with very extensive surface calcrete and dolomite. The vegetation is a short, arid thornveld that is floristically and structurally distinct from the surrounding woodlands on deep Kalahari sand. The most closely related existing vegetation type in terms of habitat type, Ghaap Plateau Vaalbosveld, is compositionally and structurally unrelated to this vegetation unit and therefore there are no grounds for extending the Ghaap Plateau Vaalbosveld vegetation type to include the vegetation of the Morokweng karstland. **Vryburg Thornveld** (Figure 9) occupies the headwaters of the Molopo River catchment that is characterised by incised/eroding landscapes along stream margins. Exposed dorbank and calcrete (along streams) occurs. Frequent springs, decanting from the neighbouring Ghaap Plateau, support hydromorphic grasslands and wetlands in the valley bottoms. The vegetation here is sparse woodland dominated by very tall *Vachellia erioloba* trees and scattered low *Vachellia hebeclada* thickets. Most of the broad-leaved woody elements and dense woodland structure of the related Mafikeng Bushveld are absent. Whilst **Vryburg Thornveld** exists as a vegetation type name in Bredenkamp and Brown (2003a), **Morokweng Thornveld** is an entirely novel derivation named after the town located in this vegetation type. **Central Sandy Mountain Bushveld** includes the vegetation on mountains and koppies currently included within the Central Sandy Bushveld vegetation type. The definition of Central Sandy Bushveld is refined to include only the plains vegetation type within the current delimitation of the vegetation type on soils derived from igneous rocks. Vegetation on vertic clay soils within the current delimitation of Central Sandy Bushveld are reassigned to Springbokvlake Thornveld. This split of central sandy woodland vegetation in mountain bushveld and (plains) bushveld also aligns better to the vegetation type model developed here.

Table 7. Summary of the changes made to the North West province vegetation map. Changes are summarised according to the potential type of changes described in the South African National Ecosystem Classification System Handbook* (SANBI 2023) (continued)

No.	Types of change
	Central Sandy Mountain Bushveld is being reinstated as a vegetation type having been grouped with Central Sandy Bushveld in the National Vegetaiton Map since 2006. It is a well-established vegetation type recognised by several previous authors. It is synonymous with Van der Meulen's *Combretum molle – Diheteropogon amplectens* order described in his vegetation map of the western Transvaal bushveld (Van der Meulen & Westfall 1979); Brown's *Pappea capensis – Combretum apiculatum* (mountain) bushveld vegetation type described for the vegetation study of the Borakalalo Nature Reserve (Brown & Bredenkamp 1994; Brown et al. 1995, 1996 and 1997); and Bredenkamp and Brown's (2003a) Mogosane Mountain Bushveld and Central Mixed Bushveld vegetation types in their vegetation map of the NW. The rationale for why this unit was not incorporated into the 2006 National Vegetation Map is not recorded anywhere.
MJ3	**Reassignment of a community in a vegetation type from an existing vegetation type to another existing vegetation type** Not applicable.
MJ4	**Extension of the range of an existing vegetation type far beyond the current extent (to be determined by committee)**
	See MN6 above.

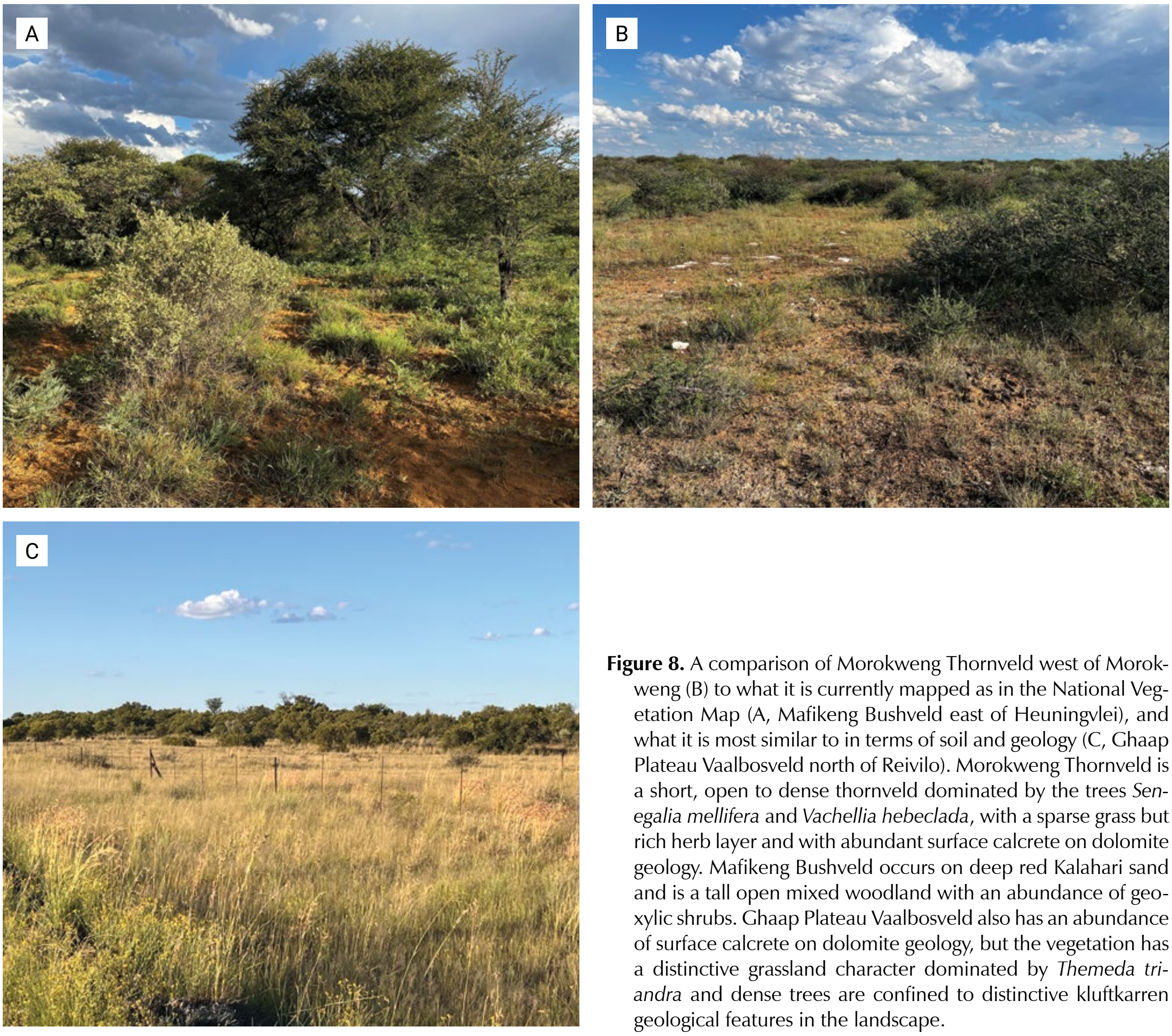

Figure 8. A comparison of Morokweng Thornveld west of Morokweng (B) to what it is currently mapped as in the National Vegetation Map (A, Mafikeng Bushveld east of Heuningvlei), and what it is most similar to in terms of soil and geology (C, Ghaap Plateau Vaalbosveld north of Reivilo). Morokweng Thornveld is a short, open to dense thornveld dominated by the trees *Senegalia mellifera* and *Vachellia hebeclada*, with a sparse grass but rich herb layer and with abundant surface calcrete on dolomite geology. Mafikeng Bushveld occurs on deep red Kalahari sand and is a tall open mixed woodland with an abundance of geoxylic shrubs. Ghaap Plateau Vaalbosveld also has an abundance of surface calcrete on dolomite geology, but the vegetation has a distinctive grassland character dominated by *Themeda triandra* and dense trees are confined to distinctive kluftkarren geological features in the landscape.

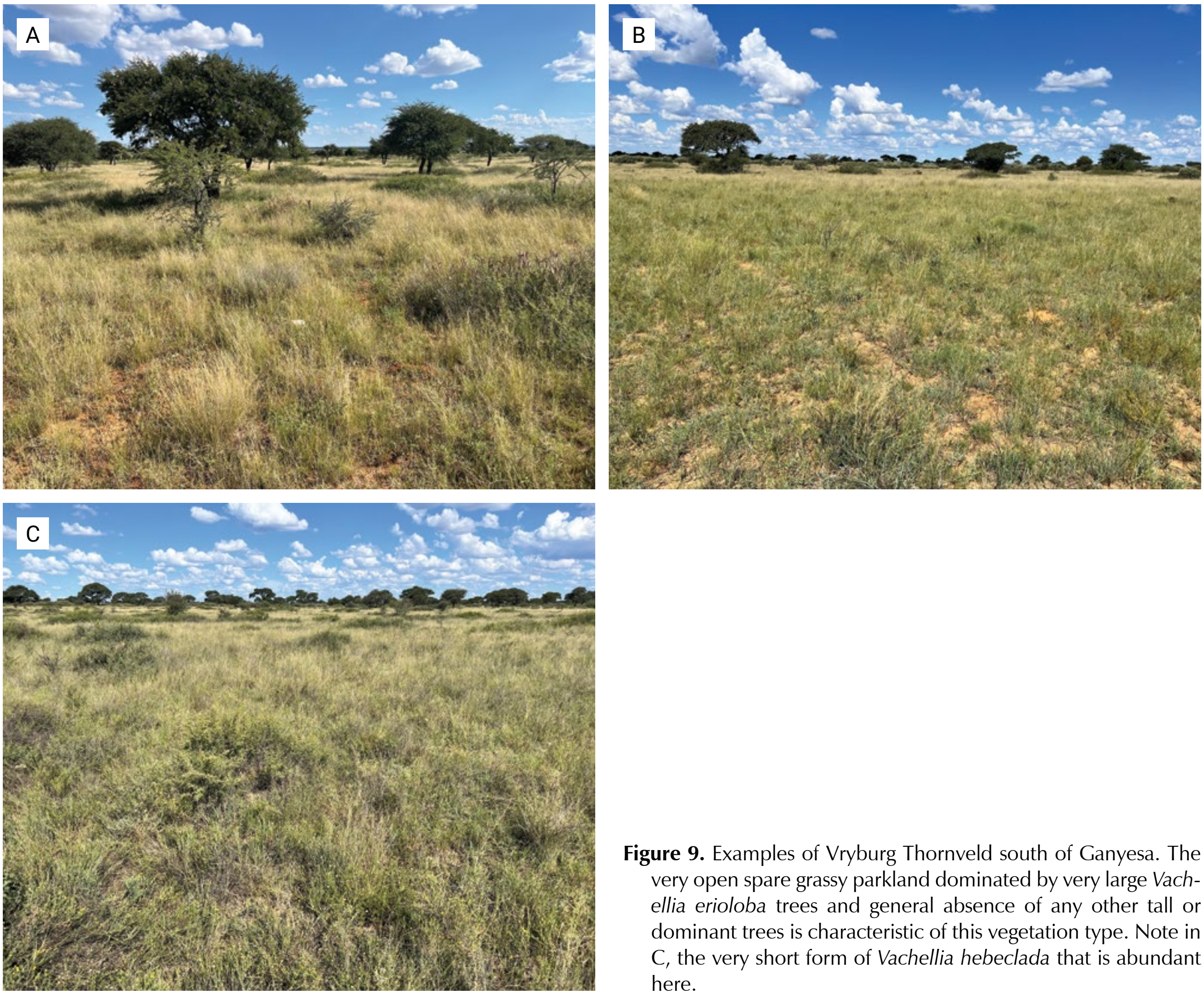

Figure 9. Examples of Vryburg Thornveld south of Ganyesa. The very open spare grassy parkland dominated by very large *Vachellia erioloba* trees and general absence of any other tall or dominant trees is characteristic of this vegetation type. Note in C, the very short form of *Vachellia hebeclada* that is abundant here.

Revised vegetation map

The revised vegetation map contains 1 810 polygons compared to the current vegetation map that has 159 polygons (Figure 10). Whilst the vegetation type concepts remain mostly unchanged from Mucina and Rutherford (2006), polygon boundaries have been entirely remapped, and this has resulted in significant changes in extent from most vegetation types (Table 8). The remapping of boundaries is an inevitable product of the much higher resolution mapping informants available to this project, as well as the application of the vegetation type identification key.

Updated descriptions of North West terrestrial vegetation types

The vegetation type descriptions have been updated (Supplementary Material 2: Vegetation type descriptions) to reflect new data available and to better align with the vegetation type identification key (Table 6). Descriptions are based on the original descriptions that appear in Mucina and Rutherford (2006) and where necessary these have been updated based on the inputs presented in Table 9.

Discussion

The revised vegetation map is significantly changed mainly with respect to where the boundaries of vegetation types are mapped. Whilst there are some changes proposed to the classification of vegetation types, for the most part, the current vegetation type concepts remain unchanged. The change in the mapping of vegetation type boundaries is an inevitable result of: (1) a clearer understanding of vegetation determinants (i.e., vegetation type classification framework or identification key); and more importantly, (2) the much-increased resolution and availability of mapping informants. It is very important to note that the significant change in mapped boundaries does not suggest or imply in any way that the current vegetation type concepts are invalid.

The vegetation identification key is important for informing the current vegetation map revision. It also

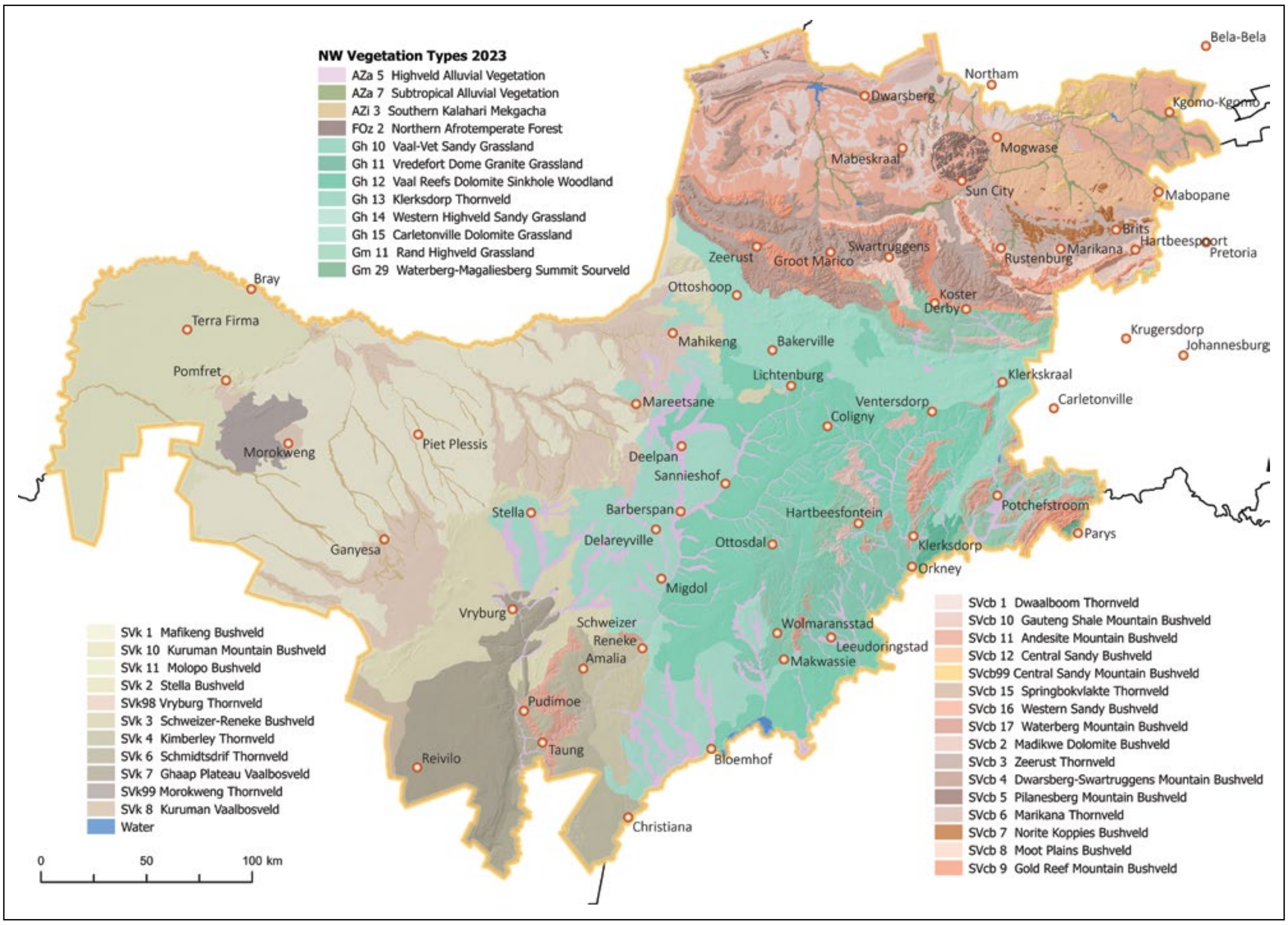

Figure 10. The revised 2023 vegetation map of the North West province (NW). The legend colour scheme follows that of the existing National Vegetation Map (NVM).

Table 8. Summary of the change in extent of South African vegetation types between the 2006 (2018) National Vegetation Map (NVM) and the 2023 revised North West province (NW) vegetation map

Mapcode	SA vegetation type name	Area (ha)		% Change 2006 to 2023
		NVM 2006	NW 2023	
AZa5	Highveld Alluvial Vegetation	175 789	424 274	141
AZa7	Subtropical Alluvial Vegetation		67 979	
AZi3	Southern Kalahari Mekgacha	22 392	126 031	463
FOz2	Northern Afrotemperate Forest	634	2 279	260
Gh10	Vaal-Vet Sandy Grassland	809 573	1 051 812	30
Gh11	Vredefort Dome Granite Grassland	5 354	4 449	-17
Gh12	Vaal Reefs Dolomite Sinkhole Woodland	29 856	26 543	-11
Gh13	Klerksdorp Thornveld	393 029	320 207	-19
Gh14	Western Highveld Sandy Grassland	858 938	675 345	-21
Gh15	Carletonville Dolomite Grassland	643 165	570 810	-11
Gm11	Rand Highveld Grassland	282 159	265 257	-6
Gm29	Waterberg-Magaliesberg Summit Sourveld	2 060	2 160	5
Gm8	Soweto Highveld Grassland	6 951		-100
SVcb1	Dwaalboom Thornveld	552 034	274 473	-50

Table 8. Summary of the change in extent of South African vegetation types between the 2006 (2018) National Vegetation Map (NVM) and the 2023 revised North West province (NW) vegetation map (continued)

Mapcode	SA vegetation type name	Area (ha)		% Change 2006 to 2023
		NVM 2006	NW 2023	
SVcb10	Gauteng Shale Mountain Bushveld	16 907	64 636	282
SVcb11	Andesite Mountain Bushveld	63 753	179 521	182
SVcb12	Central Sandy Bushveld	259 079	304 120	17
SVcb99	Central Sandy Mountain Bushveld		29 247	
SVcb15	Springbokvlakte Thornveld	157 706	22 489	-86
SVcb16	Western Sandy Bushveld	104 103	409 672	294
SVcb98	Western (Eastern) Sandy Bushveld		114 866	
SVcb17	Waterberg Mountain Bushveld		523	
SVcb2	Madikwe Dolomite Bushveld	74 839	83 900	12
SVcb3	Zeerust Thornveld	412 599	131 322	-68
SVcb4	Dwarsberg-Swartruggens Mountain Bushveld	264 463	412 887	56
SVcb5	Pilanesberg Mountain Bushveld	43 464	36 792	-15
SVcb6	Marikana Thornveld	151 015	126 150	-17
SVcb7	Norite Koppies Bushveld	21 859	41 946	92
SVcb8	Moot Plains Bushveld	249 632	139 696	-44
SVcb9	Gold Reef Mountain Bushveld	128 104	229 978	80
SVk1	Mafikeng Bushveld	1 401 610	1 122 451	-20
SVk10	Kuruman Mountain Bushveld	23 811	123 195	417
SVk11	Molopo Bushveld	1 569 288	1 015 032	-35
SVk2	Stella Bushveld	322 284	476 445	48
SVk3	Schweizer-Reneke Bushveld	202 752	133 540	-34
SVk4	Kimberley Thornveld	482 231	190 398	-61
SVk6	Schmidtsdrif Thornveld	44 792	66 082	48
SVk7	Ghaap Plateau Vaalbosveld	638 861	413 785	-35
SVk8	Kuruman Vaalbosveld	75 225	45 689	-39
SVk98	Vryburg Thornveld		648 532	
SVk99	Morokweng Thornveld		100 159	

serves a far greater purpose beyond just this vegetation map revision. Firstly, it enables users of the vegetation map to clearly understand how vegetation is assigned to different vegetation types and therefore users can apply the classification framework to mapping vegetation at finer spatial scales. When mapping vegetation at the provincial scale there are time and budget constraints limiting the amount of detail that can be mapped relative to what can be observed in the informants. It is not practically possible to manually map vegetation at infinitely fine scales over large regions. Therefore, there are inherent boundary or misclassification errors in the final map product due to mapping scale. Using the vegetation type identification key it is possible for users of the map to apply the classification framework at a fine or local spatial scale to improve mapping accuracy or interpretation for specific purposes, for example, fine-scale vegetation mapping for environmental impact assessments.

Secondly, the identification key can illuminate inconsistencies in the current vegetation type classification and

Table 9. Summary of the inputs used to update the vegetation type descriptions

Distribution	Where appropriate the description of vegetation type distribution within the NW has been updated to reflect the distribution as represented in the revised vegetation map
Altitude	Altitudinal ranges are updated for the NW based on the elevation derived from the Aster GDEM.
Vegetation and landscape features	Updated with Bredenkamp and Brown (2003a) and the authors observations.
Geology and soils	Updated with authors observations, Bredenkamp and Brown (2003a), agricultural land types and simplified geology. The lithostratigraphic geological descriptions used in the current vegetation type descriptions are dispensed with in favour of simplified descriptions of basic geological rock types that link more closely geology, general physical and chemical properties, e.g. quartzite, basalt, granite, etc.
Climate	Climate data is not added here as this information is deemed to remain unchanged from that published in Mucina and Rutherford (2006).
Important taxa	Is based on Bredenkamp and Brown (2003a), NVD relevé data, vegetation plots collected as part of this project and authors observations. Only species that are considered to be important for identifying or differentiating the vegetation type are listed. The original and more detailed list of important taxa as published in Mucina and Rutherford (2006) are dispensed with here as these tend to be lists of all taxa encountered in a vegetation type rather than being diagnostic or characteristic species of the vegetation type or specific communities with a vegetation type. Feedback from stakeholders has indicated that these lists contain little value in terms of understanding the structure and composition or differentiating vegetation types. Important taxa are listed in order of abundance or dominance (d = dominant species) where this data is available in existing descriptions. Where this information is not available species are listed alphabetically.
Conservation	Is not discussed here as this would require consideration of the extent of vegetation types outside of the province, as well as compilation of an updated landcover and protected area database. This analysis would be better addressed once this vegetation map has been integrated with the National Vegetation Map.
Remarks	Updated with authors and stakeholders' observations. Included here are observations regarding further work that needs to be done to clarify/update the vegetation type definition, description or mapping.
References	Updated with relevant references post Mucina and Rutherford (2006) and includes unpublished reports.

thus identify where vegetation types could be split, aggregated or new ones defined. For example, one such inconsistency highlighted with this project relates to the definition and mapping of Central Sandy Bushveld. This vegetation type contains both plains and mountain habitat, as well as several major geological rock types (granite and quartzite/sandstone). It is likely that applying a similar vegetation type classification as used here to elsewhere in South Africa will identify inconsistencies in the definition and mapping of vegetation types.

A stated objective of this project was to conduct a quantitative floristic analysis to find support for the vegetation type concepts using the available relevé database. This objective was not achieved within the allocated project time period. Quantitative floristic analysis to validate the vegetation type concepts used in the National Vegetation Map is a major research gap that should be addressed not only for the NW, but also more broadly in South Africa. These analyses should be earmarked as a future research priority.

There is some support in the literature for the vegetation type concepts as framed in the vegetation type identification key. For example, the Bredenkamp and Brown (2003b) analysis of the Bankenveld area supports the mountain vs plains vegetation distinction, as well as separation of grasslands based on moisture availability, soil texture and depth. Within the mountain category, vegetation units are separated based on aspect and elevation rather than geological rock type. This does suggest that within the current vegetation type classification there will be a necessary and pragmatic trade-off between ecological units that are easy to map and identify (viz. discrete mountains with similar geology) versus phytosociologically correct units that are more complex to map (viz. aspect and elevation gradients). Similarly, the Winterbach (1998) and Winterbach et al.

(2000) analysis of the Arid Sweet Bushveld region also supports the major environmental divisions associated with higher-order vegetation associations, namely, clay vs sandy soils on plains, and plains vs mountains. Both these studies suggest that it is highly likely that the current vegetation type concepts can be supported and further refined through quantitative floristic analysis.

A deficit of observations on the iNaturalist app for the NW was noted. iNaturalist is a very accessible and practical tool for collecting and identifying biodiversity information. Two training workshops were held with DEDECT officials to introduce them to the potential of the iNaturalist and the Carrymap apps. Within the province the iNaturalist app could have future applications for gathering biodiversity data, monitoring environmental compliance; to improve decision making in the EIA process; and to monitor the distribution of invasive alien species. Within the context of this study, iNaturalist proved very useful for capturing and linking field observations to a national database. Species observations in iNaturalist were uploaded together with context photographs of the vegetation type and linked to an iNaturalist National Vegetation Map project managed by SANBI. This project is using iNaturalist to collect representative photographs of all South African vegetation types.

An interesting observation with regards the species data is the large disparity between observations collected via survey plots versus herbarium records. Nearly 40% of the province's flora has never been recorded in a vegetation survey plot. This observation can be partly due to the fact that surveying flora for vegetation analysis (i.e., relevés) tends to under report or omit uncommon and rare species. This observation can also be due to under sampling of the province for vegetation analysis. The very low sampling density of relevés; the tendency for samples to be clumped rather than uniformly distributed; and the disparity in species records between herbarium versus plot data would suggest that from a vegetation description and analysis perspective that the NW is significantly under sampled. As highlighted above there is still a need for further floristic surveys and analysis to better understand and describe our vegetation types.

This revision of the NW vegetation map has focused on the terrestrial ecosystems of the province and therefore the descriptions of 'azonal' ecosystems are not updated here. Consideration of these ecosystems is, however, central to the mapping process, as well as understanding of terrestrial ecosystems. In the mapping process these ecosystems are generally always mapped first as they are often the easiest units to identify, more importantly they provide a concrete starting point for interpreting the input data in relation to the identification key and ultimately understanding vegetation/landscape patterns. The NW has for the most part relatively flat landscapes that support wide floodplain/alluvial ecosystems and extensive endorheic pan ecosystems. The province also straddles three major biogeographic regions that influence the vegetation composition of these ecosystems. Therefore, there is a great extent and diversity of azonal systems, and it has been necessary to map the larger occurrences of these ecosystems to have more consistent environmental and floristic definitions of terrestrial ecosystems.

In the revised vegetation map the extent of azonal ecosystems has been significantly extended from the 198 000 ha or 2% in the 2006 vegetation map to 618 000 ha or 6% of the province in the present map. Mapping has focused on azonal ecosystems associated with drainage lines and there has been no attempt to map endorheic pan systems except where these are associated with drainage lines.

It must be noted that during this project there was extensive discussion amongst stakeholders of the appropriateness of the term 'azonal'. In the NW context these ecosystems include all ecosystem types where the occasional occurrence of surface water and waterlogged soils is amongst the primary environmental determinants of ecosystem structure, function and definition. The term azonal could apply to any ecosystem with limited extent or that occurs widely across the landscape as a distinct feature within other ecosystems. The term is also discriminatory towards aquatic/wetland ecosystems as azonal can imply ecosystems of lesser importance or status. In the terrestrial realm collective terms such as grassland or savanna are used to group ecosystems. These terms are broadly descriptive of the nature of the contained ecosystems. Conversely, the term azonal in the context of the NW vegetation map does not convey the very important fact that the contained ecosystems are all determined and driven by water and hydrological processes. Whilst the use of the term 'azonal' is retained here, it is highly recommended that a new collective term for ecosystems driven by water be sought that is accepted by other terrestrial and aquatic/wetland ecologists. For the three azonal ecosystems considered in the NW vegetation map, the term 'alluvial' ecosystems would be a much more appropriate descriptive name.

Azonal ecosystems have been grouped into three existing ecosystem types, each associated with the three major river catchments/bioregions of the province. They are:

1. AZa 5 Highveld Alluvial Vegetation in the Highveld/Vaal River catchment including AzF3 Eastern Temperate Freshwater Wetlands.
2. AZi 3 Southern Kalahari Mekgacha in the Kalahari/Molopo River catchment.
3. AZa 7 Subtropical Alluvial Vegetation in the Bushveld/Crocodile River catchment.

Notable fluvial landscapes of the province include:

1. Kgomo-Kgomo/Tswaing area has extensive grassland floodplains (AZa 7 Subtropical Alluvial Vegetation) associated with several rivers flowing northwards out of Gauteng into the Pienaars/Moretele River and includes the Apies, Tshwane and Kutswane rivers. These floodplain ecosystems are unique within the NW and possibly within the Bushveld Bioregion. The only other area in South Africa with similar floodplain ecosystems is the Nylsvlei in Limpopo. Unfortunately, these ecosystems are being heavily impacted by sprawling peri-urban and rural settlements. This area is in great need of conservation action, as well as wetland rehabilitation.
2. The *Senegalia galpinii* riparian gallery forest on the Crocodile River, where the Moretele River enters, is one of the most iconic AZa 7 Subtropical Alluvial Vegetation riparian communities in the province.
3. The Mooi River catchment above the Klerkskraal Dam is possibly the largest and most intact mesic fluvial system on the western Highveld (mapped as AZa 5 Highveld Alluvial Vegetation in this map and as Temperate Freshwater Wetlands in the 2006 vegetation map), and as such should receive greater conservation focus, as it is essentially the last remaining intact grassland catchment landscape on the western Highveld.
4. Very extensive grassland floodplain systems (AZa 5 Highveld Alluvial Vegetation) are mostly associated with Gh 14 Western Highveld Sandy Grassland. These fluvial systems cover nearly 250 000 ha. Distinct features of these fluvial systems are the presence of surface calcrete; the general lack of well-defined river channels; and are often associated with networks of pans indicative of palaeo-river channels (mapped as AZi 10 Highveld Salt Pans in the SA Vegetation Map); and the singular dominance of the tree *Searsia lancea*.
5. A defining environmental characteristic of AZi 3 Southern Kalahari Mekgacha is the presence of surface calcrete indicating the ‘riverbed’. A unique vegetation feature associated with this calcrete not identified by previous authors is the abundance of species with Nama Karoo affinities such as *Pentzia incana* (Asteraceae), *Ruschia griquensis, Ruschia semidentata, Ruschia spinosa* (Aizoaceae) and various Zygophyllaceae and Acanthaceae. This is the only vegetation type within the Kalahari bioregion where succulent taxa are encountered in any abundance and represents the only major incursion of Nama Karoo biome affinities into the NW and the Savanna biome.

Much of south-central NW has been ploughed for crop production and this makes observing vegetation type boundaries on the ground, or at least where they used to occur, almost impossible to observe. This is particularly difficult across the transitions of Highveld grassland types that are the primary target of cultivation. Whilst these boundaries are not clearly observable today, having a clear vegetation–environment model does make predicting where these boundaries are likely to be much easier. This reinforces the importance of having such a model for mapping and describing vegetation types, and it would be beneficial if this model could be extended to include all vegetation types in South Africa.

Conclusions

The revised vegetation map of the NW is a significant improvement on the 2018 National Vegetation Map and has been incorporated into the current NVM 2024 beta release. Firstly, the vegetation type classification model based on five broad environmental variables (flooding, bioregion, terrain, geology and soil) provides a consistent and explicit framework for understanding the distribution and hence mapping vegetation types. Whilst agricultural land types remain a good proxy for mapping vegetation, breaking these units down in their underlying environmental determinants (soil and topography) and mapping these provide better proxies for mapping vegetation. Secondly, the abundance of high-resolution remote sensing products, relative to the 1980s when land types were mapped, means that vegetation type boundary accuracy is significantly improved. Thirdly, although a quantitative phytosociological analysis was not able to be completed, based on the description of existing vegetation types, the available literature, stakeholder inputs and field observations, the current vegetation type concepts are valid units. It was necessary, however, to elevate three previously described vegetation concepts as new vegetation types to accommodate observable vegetation patterns in the landscape and also to align with the vegetation classification model.

It is recommended that the existing azonal vegetation type category be replaced with the term alluvial for the three azonal vegetation types in the NW where occasional flooding or waterlogging is a primary determinant of vegetation. This alluvial vegetation type unit also contains the majority of wetlands in the province.

This will not be the last word on the mapping of vegetation in the NW. Despite the wealth of phytosociological literature available for the province, there are still major gaps in our descriptive vegetation science knowledge in the province. Also, there is no research at all that relates phytosociological vegetation concepts to the modern South African vegetation type concepts, and the vegetation classification model or framework developed here might provide the basis for developing a similar framework for the entire country. Given the importance of vegetations types in environmental policy, planning and decision making, having clear, consistent and defensible environmental definitions for vegetation types will help practitioners identify and map vegetation types on the ground.

Acknowledgements

This project was entirely funded by the North West Provincial Government Department of Economic Development, Environment, Conservation and Tourism (Project number DEDECT 06/2021). The South African National Biodiversity Institute (SANBI) provided extensive technical support to the project, as well as facilitated access to data and contributed to fieldtrip expenses. We are grateful to the members of the project steering committee for their support and inputs on the project design and execution, namely, Tharina Boshoff, Adriaan van Straaten, Aluwani Tshiila, Malefyane Mosadi, Doug Macfarlane, Leo Quayle, Ryan Kok and Willem Boshoff. Many individuals provided valuable technical inputs, datasets or comments on the vegetation map, namely, Andrew Skowno, Nacelle Collins, Lorraine Mills, George Bredenkamp, Jacobus Smit, Marc Stalmans, Tony de Castro, Noel van Rooyen, Naas Grové, David Hoare and Leslie Brown. The members of the National Vegetation Map Committee who reviewed and commented on the draft manuscript are thanked for their insights: Tony Rebelo, Debbie Jewitt, Andrew Skowno and Kagiso Mogajane.

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Supplementary material

Supplementary material 1:
Annotated plant checklist for the North West province

Only available online: http://dx.doi.org/10.38201/btha.abc.v54.10

Supplementary material 2:
Vegetation type descriptions

1. FOz 2 Northern Afrotemperate Forest

Distribution	In the North West province (NW) forest is restricted to mesic fire-free sites on the Magaliesberg with small, scattered patches in the Pilanesberg, Swartruggens and on the Enzelsberg.
Altitude	Most patches occur at altitudes between 1 600 and 1 700 m.
Vegetation and landscape features	Low (in the Low Escarpment region with canopy reaching up to 20 m), relatively species-poor evergreen forests of afromontane origin and some of them still showing clear afromontane character. Found as small patches in kloofs and on subridge scarps typically in rock and bolder scree slopes.
Geology and soils	The Magaliesberg is comprised primarily of rough, large-grained quartzite, which weathers to coarse and shallow sandy soil. This supports mostly open savanna and grassland. However, there are a number of ravines/kloofs on north-facing slopes, as well as steep slopes on south-facing slopes that provides some protection from fires. Forests on the north-facing slopes are restricted to well-defined kloofs/ravines with sharp boundaries. Other conditions in these kloofs that contribute to the development of forests are the accumulation of deep soils (in contrast to the very shallow, coarse, sandy soils in most of the Magaliesberg), and the presence of perennial streams and moist seepage zones.
Important taxa	**Species of the north-facing slopes**: *Calodendrum capense* (d*), *Celtis africana* (d), *Diospyros whyteana* (d), *Englerophytum magalismontanum* (d), *Ficus burkei* (d), *Empogona lanceolata* (d), *Maytenus undata* (d), *Ochna holstii* (d), *Acokanthera oppositifolia, Apodytes dimidiata, Cussonia transvaalensis, Halleria lucida, Ilex mitis, Olea capensis* subsp. *enervis, Olea europaea* subsp. *cuspidata, Mimusops zeyheri, Olinia emarginata, Prunus africana, Rauvolfia caffra, Rothmannia capensis, Scolopia mundii, Secamone alpini, Solanum giganteum, Trema orientale, Vangueria bowkeri*. **Species of the south-facing slopes**: *Acalypha glabrata* var. *glabrata* (d), *Buddleja saligna* (d), *Celtis africana* (d), *Senegalia ataxacantha* (d), *Olea europaea* subsp. *cuspidata* (d), *Calodendrum capense, Dovyalis zeyheri, Maytenus undata, Myrsine africana, Pittosporum viridiflorum, Secamone alpini, Senegalia caffra, Solanum giganteum, Vangueria bowkeri*.
Remarks	**Biogeography**: The forests of the Magaliesberg are classified as Northern Afrotemperate Forests, together with the forests of the Waterberg in the current vegetation map, but the floristic composition of the forests in these mountain ranges is significantly different. Some species occur exclusively in the Magaliesberg (but not in the Waterberg) and vice versa. For instance, *Podocarpus latifolius* and *Curtisia dentata* are dominant species in many Waterberg forests, but these species are absent from the Magaliesberg. Conversely, species with a tropical affinity such as *Rauvolfia caffra* occur in the Magaliesberg, but not in the Waterberg. Both these forests are considered to be relic forests, as they are representative of communities that would have been more common under a former wetter climate. In the Magaliesberg, the presence of isolated specimens of species such as *Psydrax obovata* subsp. *elliptica* and *Scolopia mundii*, which are normally associated with high-rainfall escarpment habitats, provides some evidence for this.

*d = dominant species, see Table 9 in main text.

Remarks (continued)	**Vegetation dynamics**: Based on aerial and satellite image interpretation of the same areas over several decades, between the 1930s and 1940s to the present day, it is clear that the area covered by woody vegetation is expanding. This could be primarily attributed to protection from burning. Evidence of this expansion includes the presence of trees in dense forests that would ordinarily be dependent on germination and development in open habitats. Examples include large specimens of *Erythrina lysistemon* and *Senegalia ataxacantha* inside closed forests, as well as the presence of dense stands of forest pioneers such as *Trema orientalis* on the margins of some forests. The presence of extensive Olea Sclerophyllous Forest with its low tree species diversity could also be an indication of expanding forests with this distinct and widespread forest community forming a primary forest succession phase. **Conservation and utilisation**: Most of these forests are well-protected, being situated on private land where access is restricted. The primary uses are conservation, recreation, and for ecosystem services, e.g., sustainable water production. Many farming areas north of the Magaliesberg are dependent on the harvesting of water from the north-facing kloofs. Many of the kloofs are used for hiking throughout the year. The Mountain Club of South Africa's kloofs are accessible to members and to the public through permits. There is little evidence of current or historical exploitation. The only exception is Majakaneng Kloof, which is owned by a community property association, and where trees are heavily harvested for medicinal use. Forests on south-facing slopes tend to develop in moist, fire-protected positions in south-facing gullies and steep slopes below the cliffs with boulder and rock scree, where they are well-protected against fire. The forests on south-facing slopes, being drier and cooler, have a different floristic composition to the wetter kloof forests of the north-facing slopes. The forests on south-facing slopes tend to dominate on the higher altitudes just below the cliffs, and often grade into dense Olea Sclerophyllous Forest comprising *Olea europaea* subsp. *cuspidata, Celtis africana, Ziziphus mucronata* and *Buddleja saligna,* with no clear distinction between the boundary of the two forest types. However, Olea Sclerophyllous Forest is much less diverse in species, and often completely dominated by *Olea europaea* subsp. *cuspidata*. This forest type or community is widespread in the NW, as well as other parts of South Africa from the Eastern Cape to the northern provinces. It is typically found in fire refuges on deeper soils such as alluvial soils (bottom slope) or rock scree slopes (top slope). In the NW well-developed examples of this unit are found in the Magaliesberg, often associated with Northern Temperate Forests; dolines in Carletonville Dolomite Grassland; valleys in the Dwarsberg-Swartruggens Mountain Bushveld; and on koppies throughout the Bankenveld region.
References	Roberts (1961), Van Vuuren (1961), Killick (1963), Van Vuuren and Van der Schijff (1970), Van Zinderen Bakker (1971, 1973), Coetzee (1974, 1975), Van der Meulen (1978, 1979), Bredenkamp and Theron (1978, 1980), Westfall (1981), Cooper (1985), Westfall et al. (1984), Everard (1986), Behr and Bredenkamp (1988), Du Preez and Bredenkamp (1991), Du Preez (1991), Smit et al. (1993), Hill (1996), Eckhardt et al. (1997), Ellery et al. (2001), Siebert (2001), Van Staden (2002), Von Maltitz et al. (2003), Van Staden and Bredenkamp (2005, 2006), Geldenhuys and Mucina (2006).

2. Gh 10 Vaal-Vet Sandy Grassland

Distribution	North West and Free State provinces, south of Lichtenburg and Ventersdorp, stretching southwards to Klerksdorp, Leeudoringstad, Bothaville and to the Brandfort area north of Bloemfontein.
Altitude	1 200–1 620 m (median 1 420 m).
Vegetation and landscape features	Dry, medium (0.75–1.00 m) tussock grassland dominated by *Themeda triandra* with a karroid shrub element. In pockets of deeper sand Kalahari elements, such as stands of *Vachellia erioloba*, are present.
Geology and soils	Mostly Kalahari sand aeolian deposits with some colluvial soils overlaying various geologies. Dominant land types Bc and Bd with soil forms mostly Avalon, Westleigh and Clovelly. Red, eutrophic, plinthic soils, depth 0.5–1.0 m, average clay content 15–20%
Important taxa	**Grasses**: *Themeda triandra* (d*), *Anthephora pubescens* (d), *Eragrostis lehmanniana* (d), *Aristida congesta, Brachiaria serrata, Cynodon dactylon, Eragrostis curvula, E. superba, Panicum coloratum, Tragus berteronianus, Triraphis andropogonoides.*

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*d = dominant species, see Table 9 in main text.

Important taxa (continued)	**Shrubs**: *Asparagus laricinus* (d). **Herbs**: *Felicia muricata* (d), *Pentzia globosa* (d), *Selago densiflora, Hibiscus pusillus, Ledebouria marginata*.
Remarks	Key identifying features of this vegetation type is the presence of *Asparagus laricinus*, as well as the abundance of narrow-leaf ironbark eucalyptus (*Eucalyptus crebra*) woodlots. These species are indicative of deep, freely draining, sandy soils. The absence of these woodlots is especially useful when marking the transition to Gh 14 Western Highveld Sandy Grassland. Pockets of aeolian sand in neighbouring vegetation units tend to contain Vaal-Vet Sandy Grassland. This is especially observable in Gh 15 Carletonville Dolomite Grassland. Locally, low cover of *Themeda triandra* and the associated increase in *Elionurus muticus, Cymbopogon pospischilii* and *Aristida congesta* is attributed to heavy grazing. *Seriphium plumosum* or bankrupt bush can also be prevalent in overgrazed situations. The bush encroaching tree species in this vegetation unit is *Vachellia karroo*. This vegetation type is highly suitable for cultivation, and it is currently extensively cultivated. In its definitive form occurring on deep soils on gentle gradients there are no impediments to ploughing and it is likely that this type has been largely eradicated by cultivation and is most likely extinct. Any intact examples of this vegetation unit that remain would be very important conservation targets.
References	Louw (1951), Morris (1973, 1976), Bredenkamp and Bezuidenhout (1990), Kooij (1990), Bezuidenhout and Bredenkamp (1991a), Kooij et al. (1990, 1992), Bezuidenhout et al. (1994a).

3. Gh 11 Vredefort Dome Granite Grassland

Distribution	Free State and North West provinces, central portion of the Vredefort Dome around Parys and Vredefort.
Altitude	1 330–1 540 m (median 1 400 m).
Vegetation and landscape features	Moderately undulating plains with medium (0.5–0.75 m) tussock grassland. Plains are interspersed with large granite-domed koppies.
Geology and soils	Coarse textured colluvial soils derived from the underlying granite bedrock. Ba land type with red dystrophic plinthic soils (Hutton, Mispah, Avalon forms), average depth < 0.5 m, average clay 20%.
Important taxa	**Grasses**: *Themeda triandra* (d*), *Elionurus muticus* (d), *Setaria sphacelata* var. *torta* (d), *Brachiaria serrata, Cymbopogon pospischilii, Eragrostis chloromelas, E. racemosa, Heteropogon contortus, Trichoneura grandiglumis*. **Forbs**: *Barleria macrostegia, Helichrysum rugulosum, Hermannia depressa, Polygala hottentotta, Scabiosa columbaria, Turbina oblongata*.
Remarks	Vredefort Dome is an interesting geological structure – a strongly eroded remnant of one of the largest impact craters of the world, about 2.2 billion years old. This vegetation type is mostly very degraded through overgrazing and cropping. Examples of intact plains grassland are rare. Fields of bankrupt bush (*Seriphium plumosum*) are widespread.

*d = dominant species, see Table 9 in main text.

Remarks (continued)	The vegetation of the granite koppies in the vegetation type contain good examples of Olea Sclerophyllous Forest. This is a primary succession forest community that originates with the emergence of *Olea europaea* subsp. *cuspidata* from woodland vegetation to form a closed and contiguous evergreen forest cover. *Olea europaea* subsp. *cuspidata* is joined by *Celtis africana* and *Ziziphus mucronata* as dominant tree species. The development of this community is likely due to the general reduction in fire frequency in the landscape. This forest community is widespread in South Africa, encountered in most bushveld and woodland vegetation types in mesic, fire-protected positions. In terms of the vegetation type typology discussed in Results (Table 6), plains vs mountains is a key environmental discriminant of vegetation types. The woodland vegetation of the granite koppies mapped as part of this vegetation type has closer affinity to that of surrounding Gold Reef Mountain Bushveld vegetation types rather than to the grassland of this vegetation type. Therefore, these koppies should rather be grouped with the neighbouring Gold Reef Mountain Bushveld, Andesite Mountain Bushveld, or be assigned their own vegetation type.
References	Du Preez (1986), Bezuidenhout et al. (1988, 1994c), Bredenkamp et al. (1989), Du Preez and Venter (1990a, 1990b), Bezuidenhout (1993), Eckhardt et al. (1993), Fuls et al. (1992, 1993).

4. Gh 12 Vaal Reefs Dolomite Sinkhole Woodland

Distribution	NW, small area associated with the dolomite sinkholes in and around Stilfontein and Orkney (Vaal Reefs). The Vaal River forms the southern distribution limit of this vegetation unit.
Altitude	Altitude 1 280–1 380 m.
Vegetation and landscape features	Slightly undulating landscape dissected by prominent rocky chert/dolomite ridges and supporting a grassland-woodland vegetation complex. The most typical vegetation feature is the woodland, which occurs naturally in clumps around sand-filled dolines (sinkholes), which is characteristic of karst landscapes.
Geology and soils	This area occurs almost exclusively on the dolomites of the Malmani Subgroup (Chuniespoort Group, Transvaal Supergroup), where underground dissolution of the rock causes sinkholes, as well as caves. More than 50% of the main soil types are relatively shallow (50–150 mm) and rocky, with the dominant soil forms including Mispah, Glenrosa and shallow Hutton. Land type Fa.
Important taxa	**Trees**: *Vachellia erioloba* (d*), *Celtis africana* (d), *Searsia lancea* (d), *Senegalia caffra, Vachellia karroo, V. robusta* subsp. *clavigera*. **Tall shrubs**: *Diospyros lycioides* subsp. *lycioides* (d), *Ehretia rigida* (d), *Grewia flava* (d). **Shrubs**: *Asparagus suaveolens* (d), *Gymnosporia heterophylla* (d), *Pavonia burchellii* (d), *Sida dregei* (d), *Elephantorrhiza elephantina*. **Grasses**: *Aristida congesta* (d), *Digitaria eriantha* (d), *Eragrostis biflora* (d), *E. curvula* (d), *Themeda triandra* (d).
Remarks	The mapped extent of the dolomite sinkhole woodlands should be revisited at a more detailed scale than that offered by our current coverage. Clear separation (expressed in appropriate mapping coverage) between this unit and the adjacent Carletonville Dolomite Grassland is needed. These two units are closely related given the same underlying geology and soils. There is an observable gradient in tree abundance/density as one descends from the Vaal/Limpopo interfluve (Carletonville Dolomite Grassland) down into the Vaal River Valley (Vaal Reefs Dolomite Sinkhole Woodland) and the boundary between these two vegetation units is a cline rather than a clear demarcation.

*d = dominant species, see Table 9 in main text.

Remarks (continued)	Consideration should be given to updating the name of this vegetation unit. The 'sinkholes' referred to in the vegetation name are technically dolines, therefore a more technically correct name for this vegetation unit should be 'Vaal Reefs Dolomite Doline Woodland'. Aesthetically this is one of the more scenic landscapes in the western Grassland Biome having suffered less transformation relative to surrounding vegetation types and it certainly deserves high conservation priority (i.e., Highveld National Park at Potchefstroom).
References	Louw (1951), Acocks (1953, 1975, 1988), Morris (1973), Coetzee (1974), Van Wyk (1983), Van Wyk and Bredenkamp (1986), Bezuidenhout (1993), Bezuidenhout et al. (1994b, 1994c, 1994e), Siebert and Siebert (2005).

5. Gh 13 Klerksdorp Thornveld

Distribution	NW between Klerksdorp, Leeudoringstad, Wolmaransstad and Ottosdal with an outlying occurrence in the region of the Botsolano Game Reserve north of Mafikeng.
Altitude	1 240–1 580 m (median 1 380 m).
Vegetation and landscape features	Irregular undulating plains with dense to open 'Acacia' woodland clumps in a dry tussock grassland matrix.
Geology and soils	Relatively shallow, rocky, clayey colluvial soils on the foot slopes of basalt, quartzite or chert hills. Soils red eutrophic plinthic soils (Hutton form), depth < 0.5 m, average clay 20%. Land types Bc and Bd.
Important taxa	**Trees**: *Vachellia karroo* (d*), *Senegalia caffra* (d), *Celtis africana, Searsia lancea, S. pyroides, Ziziphus mucronata*. **Shrubs;** *Diospyros lycioides, Ehretia rigida, Grewia flava, Gymnosporia buxifolia*. **Grasses**: *Cynodon dactylon* (d), *Panicum coloratum* (d), *Sporobolus fimbriatus* (d), *Themeda triandra* (d), *Andropogon schirensis, Aristida congesta, Brachiaria serrata, Cymbopogon plurinodis, Digitaria eriantha, Diheteropogon amplectens, Eragrostis curvula, E. obtusa, E. superba, Elionurus muticus, Eustachys paspaloides, Heteropogon contortus, Setaria sphacelata, Sporobolus africanus, Tragus berteronianus, Triraphis andropogonoides*. **Forbs**: *Acalypha angustata, Anthospermum hispidulum, Asparagus africanus, Bulbostylis burchellii, Gnidia capitata, Helichrysum nudifolium, Hermannia lancifolia, Justicia anagalloides, Ledebouria marginata, Pavonia burchellii, Plexipus adenostachyus, Pollichia campestris, Raphionacme hirsuta, Rhynchosia totta* var. *venulosa, Solanum incanum, Teucrium trifidum, Triumfetta sonderi, Ziziphus zeyheriana*.
Remarks	The presence and dominance of *Senegalia caffra* is a defining characteristic of this vegetation type. This vegetation type grades into mountain bushveld types along a catena on steeper more rocky slopes, and with surrounding grassland types on deeper, sandier soils. Thus this vegetation type is transitional in character between Western Highveld Sandy Grassland (shallow sand with calcrete exposed), Vaal Vet Sandy Grassland (deep sandy soils with *Asparagus laricinus* dominant) and Andesite Mountain Bushveld, and therefore could be considered a grassland or bushveld vegetation type. This vegetation unit has a high grazing capacity, and this leads to overutilisation and degradation and subsequent invasion of *Vachellia karroo* into adjacent dry grassland.
References	Louw (1951), Morris (1973, 1976), Bredenkamp and Bezuidenhout (1990), Bezuidenhout (1993), Bezuidenhout et al. (1994c, 1994d), Bredenkamp and Brown (2003b).

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*d = dominant species, see Table 9 in main text.

6. Gh 14 Western Highveld Sandy Grassland

Distribution	NW from Mareetsane and Deelpan in the north to Bloemhof and Christiana in the south, west of Sannieshof and Wolmaransstad as far as Stella.
Altitude	930–1 250 m (median 1 060 m).
Vegetation and landscape features	Flat to gently undulating plains with short (< 0.5 m), dry mixed tussock/lawn grassland, with karoo shrub elements and (very) scattered woody species occurring in bush clumps. Surface calcrete can be common.
Geology and soils	Shallow Kalahari sand aeolian soil overlaying calcrete, which can be exposed in places. These recent surface deposits overlie mainly basalt geologies. Soil is red-yellow, red apedal (Hutton), soil depth < 0.5 m with a calcrete hardpan, average clay 15%. Land type Ae. Note that the bottomlands in this vegetation unit have been mostly mapped as Highveld Alluvial Vegetation in this vegetation map.
Important taxa	**Trees**: *Vachellia hebeclada, Vachellia tortilis, Diospyros lycioides*. **Grasses**: *Anthephora pubescens* (d*), *Aristida diffusa* (d), *Sporobolus africanus* (d), *Themeda triandra* (d), *A. canescens, A. stipitata, Brachiaria serrata, Digitaria argyrograpta, Diheteropogon amplectens, Elionurus muticus, Eragrostis curvula, E. gummiflua, E. racemosa, Eustachys paspaloides, Melinis nerviglumis, Setaria sphacelata, Sporobolus discosporus, S. fimbriatus, Trichoneura grandiglumis, Triraphis andropogonoides*. **Forbs**: *Chamaecrista mimosoides, Dicoma anomala, Helichrysum callicomum, Hermannia depressa, Indigofera comosa, Kyphocarpa angustifolia, Leucas capensis, Mariscus indecorus, Polygala hottentotta, Sebaea grandis, Sida dregei, Solanum panduriforme, Vernonia oligocephala*.
Remarks	Many endorheic pans (Highveld Salt Pans – not mapped here) are associated with this vegetation unit, but these have been largely included in the Highveld Alluvial Vegetation unit in this map. There is a soil depth and aridity gradient from Vaal-Vet Sandy Grassland to Western Highveld Sandy Grassland. These two grassland types are closely related floristically. The short grassland stature and presence of calcrete, and the general absence of trees and especially of the shrub *Asparagus laricinus* and *Eucalyptus* woodlots are particularly indicative of the transition to Western Highveld Sandy Grassland. This vegetation type is suitable for cultivation, but the low rainfall makes it a high-risk area for agriculture. Historically this unit was extensively cultivated, however, presently very little dryland cultivation occurs in this vegetation type. Consequently, whilst there appears to be large extents of this grassland remaining, these are mostly old-fields, and the best examples and largest extents of this vegetation type are encountered in historically communal lands. Flax-leaf fleabane (*Erigeron bonariensis*) is an alien invasive annual daisy species that is a major invader in this vegetation type leading to a loss of grassland. This is especially prevalent on commercial farms where veld fires are suppressed. It is less of a problem in communal areas. *Vachellia tortilis* and to a lesser extent *Tarchonanthus camphoratus* contribute to bush encroachment in this vegetation type.
References	Van Zyl (1965), Morris (1973, 1976), Bezuidenhout (1993), Bezuidenhout et al. (1993, 1994c).

*d = dominant species, see Table 9 in main text.

7. Gh 15 Carletonville Dolomite Grassland

Distribution	NW (mainly), Gauteng and marginally into the Free State, The karst landscape associated with the Malmani dolomite geological system stretching east–west from Centurion and Bapsfontein in Gauteng Province through to the Botswana border via Ventersdorp, Lichtenburg and Ottoshoop, with a north-south arm running from Carletonville to west of Potchefstroom.
Altitude	1 170–1 780 m (median 1 510 m).
Vegetation and landscape features	Slightly undulating plains dissected by prominent rocky chert ridges and hills dominated by medium (0.75–1.00 m) sour, wiry, tussock grasslands on the plains and woodland elements on the hills, as well as open *Protea* woodland above 1 600 m. Large depressions or dolines created from infilled sinkholes are a characteristic feature of this landscape.
Geology and soils	Dolomite and chert of the Malmani dolomites supporting mostly shallow, rocky soils. Shallow rocky soils (Mispah and Glenrosa forms), average depth 0.1–0.4 m, average clay 15%. Land type Fa. **Note**: Depressions in this landscape contain aeolian or alluvial deposits that have soils typical of the Ab land type with red to yellow apedal soils (Hutton and Clovelly forms).
Important taxa	**Grasses**: *Diheteropogon amplectens* (d*), *Loudetia simplex* (d), *Schizachyrium sanguineum* (d), *Themeda triandra* (d), *Alloteropsis semialata, Andropogon shirensis, Aristida canescens, Bewsia biflora, Elionurus muticus, Eragrostis gummiflua, Eragrostis racemosa, Monocymbium ceresiiforme, Panicum coloratum, Pogonarthria squarrosa, Triraphis andropogonoides, Tristachya leucothrix, T. rehmannii.* **Forbs**: *Bulbostylis burchelli, Dianthus mooiensis, Helichrysum miconiifolium, Indigofera comosa, Kyphocarpa angustifolia, Ophrestia oblongifolia, Parinari capensis, Searsia magalismontana, Tylosema esculentum, Protea welwitschii*.
Remarks	This vegetation type in the NW has complex phytosociological patterns as extensive recent aeolian and alluvial deposits remain in depressions in the karst landscape. The alluvial deposits in dolines are mostly associated with Olea Sclerophyllous Forest. These alluvial deposits have largely been mined for diamonds and hence there are very few intact examples of this habitat and vegetation type remaining in this landscape. The pockets of aeolian sand contain Gh 10 Vaal-Vet Sandy Grassland or Gm 11 Rand Highveld Grassland. The erratic distribution of cultivated fields throughout this vegetation type are indicative of the presence of these pockets of sand. Rock piles adjacent to cultivated lands are indicative of Carletonville Dolomite Grassland being cleared for agriculture. A characteristic feature of this vegetation type is the absence of surface water. The karst geology means most surface water drains into the bedrock below. This water discharges from the ground water around the periphery of this vegetation type where the dolomite geology makes contact with the underlying bedrock of surrounding vegetation types. This gives rise to numerous springs or 'eyes' and associated peat wetlands that are a feature of the NW landscape surrounding the various karst landscapes in the province, namely, Carletonville Dolomite Grassland, Ghaap Plateau Vaalbosveld and Morokweng Thornveld. This vegetation type forms an important catchment for most major rivers flowing in the province. Vegetation types on dolomite geology are the only types in the province where the typology includes both plains and mountain environmental groups. This definition is consistently applied to all dolomite vegetation types in South Africa and therefore the typology rule is not changed here.
References	Louw (1951), Morris (1973, 1976), Coetzee (1974), Coetzee and Werger (1975), Van Wyk (1983), Van Wyk and Bredenkamp (1986), Bezuidenhout and Bredenkamp (1990), Scogings and Theron (1990), Bezuidenhout et al. (1994b, 1994c, 1994f), Bredenkamp et al. (1994), Grobler (2000), Hartmann (2001), Siebert and Siebert (2005), Grobler et al. (2006), Daemane et al. (2010),Veldsman (2021).

*d = dominant species, see Table 9 in main text.

8. Gm 11 Rand Highveld Grassland

Distribution	Gauteng, North West, Free State and Mpumalanga provinces, slopes and valleys between rocky ridges above 1 300 m. Occurs in the NW in two areas north and south of the Malmani dolomites. In the north on the Highveld around Derby and Koster above the Swartruggens hills, and in the southeast near Potchefstroom.
Altitude	1 300–1 700 m (median 1 530 m).
Vegetation and landscape features	Wide, gently sloping valleys/plains interspersed with low ridges or hills. Tall (1 m), wiry, sour grassland in the east with shorter (0.75 m) grassland in the west. Open *Protea* woodland occurs above 1 600 m. Most common grasses on the plains belong to the genera *Themeda, Eragrostis, Heteropogon* and *Elionurus*. Low, sour shrubland and woodland on rocky outcrops and steeper slopes belongs to SVcb 9 Gold Reef Mountain Bushveld.
Geology and soils	Colluvial soils derived from underlying geology, which is varied and includes basalt/dolerite, shale/mudstone and quartzite geologies. Dystrophic and eutrophic red soils (Hutton and Clovelly forms), average depth 0.50–0.75 m, average clay 25%. Land types Ba and Bc.
Important taxa	**Eastern extent**: **Grasses**: *Cymbopogon caesius* (d*), *C. plurinodis* (d), *Eragrostis curvula* (d), *Themeda triandra* (d), *Aristida congesta, Brachiaria serrata, Cynodon dactylon, Eragrostis racemosa, E. superba, Heteropogon contortus, Setaria sphacelata var. torta*. **Forbs**: *Anthospermum hispidulum, Felicia muricata, Graderia subintegra, Helichrysum miconiifolium, H. nudifolium, Hermannia depressa, Hibiscus pusillus, Justicia anagalloides, Lippia scaberrima, Vernonia oligocephala, Ziziphus zeyheriana*. **Western extent**: **Grasses**: *Anthephora pubescens* (d), *Eragrostis lehmanniana* (d), *Themeda triandra* (d), *Aristida congesta, Cynodon dactylon, Eragrostis curvula, E. superba, Tragus berteronianus*. **Forbs**: *Hibiscus pusillus, Ledebouria marginata, Felicia muricata* (d), *Pentzia globosa* (d), *Selago densiflora*.
Remarks	This vegetation unit is very varied and geographically disjunct and requires further investigation. Most importantly, the underlying geology of this vegetation group is very diverse. As most soils are colluvial being derived from the underlying bedrock, a closer environmental/phytosociological investigation is required to determine if this vegetation type warrants splitting based on geology and/or biogeography. Bankrupt bush encroachment is prevalent in many areas due to lack of regular fire.
References	Acocks (1953, 1975, 1988), Bezuidenhout (1988), Scogings and Theron (1990), Bezuidenhout and Bredenkamp (1991b), Coetzee (1993), Coetzee et al. (1994, 1995), Smit et al. (1997), Burgoyne et al. (2000), Grobler (2000), Grobler et al. (2006).

*d = dominant species, see Table 9 in main text.

9. Gm 29 Waterberg-Magaliesberg Summit Sourveld

Distribution	Limpopo and North West provinces and marginally into Gauteng, isolated patches on summits of the Waterberg (including the Sandrivierberge, Hoekberge, Hanglipberge and Swaershoekberge), Pilanesberg and Magaliesberg.
Altitude	Altitude 1 500–2 088 m in the Waterberg, 1 853 m in the Magaliesberg and 1 687 m in the Pilanesberg.
Vegetation and landscape features	Higher slopes and summit positions including crests, and steep rocky scarps and cliff faces, covered with grassland (and accompanying rocky outcrops) dominated by wiry tussock grasses. Patches of open *Protea caffra* savannoid vegetation and open shrubland with *Englerophytum magalismontanum* and *Ancylobothrys capensis* are common and typical of this sourveld vegetation type.
Geology and soils	Acidic sandy, loamy to gravel soil derived from coarse sandstone, quartzite, and conglomerate. Land type Ib and Fa.
Important taxa	**Trees**: *Englerophytum magalismontanum, Protea caffra* subsp. *caffra, Protea roupelliae* subsp. *roupelliae, Acacia caffra, Brachylaena rotundata, Combretum moggii, Combretum molle, Faurea saligna, Vangueria infausta, Zanthoxylum capense, Elephantorrhiza burkei, Protea gaguedi, Searsia dentata*. **Grasses**: *Loudetia simplex, Aristida transvaalensis, Bulbostylis burchellii, Coleochloa setifera, Diheteropogon amplectens, Eragrostis nindensis, Melinis nerviglumis, Schizachyrium sanguineum, Trachypogon spicatus, Tristachya biseriata*. **Shrubs**: *Ancylobothrys capensis, Lopholaena coriifolia, Passerina montana, Searsia magalismontana* subsp. *magalismontana, Acalypha angustata, Euphorbia clavarioides* var. *truncata, Euphorbia schinzii, Elephantorrhiza elephantina, Parinari capensis, Selaginella dregei, Xerophyta retinervis*.
Remarks	Embedded within this sourveld there are abundant rocky sheets found on exposed mountain tops and ridges, supporting sparse edaphic grassland/herbland with resurrection plants such as *Myrothamnus flabellifolius, Xerophyta retinervis* and *Selaginella dregei*. It is here where succulents (some endemic) of the genera *Frithia*, *Khadia* and *Delosperma* (Aizoaceae), *Adromischus* (Crassulaceae), *Anacampseros* (Anacampserotaceae) and numerous low succulent representatives of *Euphorbia* are found.
References	Acocks (1953, 1975, 1988), Coetzee (1974, 1975), Coetzee and Werger (1975), Van der Meulen (1979), Westfall (1981), Burgoyne et al. (2000), Van Staden (2002), Bredenkamp and Brown (2003a, 2003b), Van Staden and Bredenkamp (2005), Van Staden et al. (2021).

10. SVcb 1 Dwaalboom Thornveld

Distribution	Limpopo and North West provinces, flats both north and south of the Dwarsberge and associated ridges mainly west of the Crocodile River in the Dwaalboom area but including a patch around Sentrum. South of the ridges it extends eastwards from the Nietverdiend area, north of the Pilanesberg to the Northam area.
Altitude	Altitude 900–1 200 m.
Vegetation and landscape features	Plains with layer of scattered, low to medium-high, deciduous microphyllous trees and shrubs with a few broad-leaved tree species, and an almost continuous herbaceous layer dominated by grass species. *Vachellia tortilis* and *V. nilotica* dominate on the medium clays (at least 21% clay in the upper soil horizon but high in the lower horizons; on particularly heavy clays (> 55% clay in all horizons) most other woody plants are excluded and the diminutive *V. tenuispina* dominates at a height of less than 1 m above ground. On the sandy clay loam soils (with not more than 35% clay in the upper horizon but high in the lower horizons) *Senegalia erubescens* is the most prominent tree. The alternation of these substrate types creates a mosaic of different 'Acacia' woodlands.
Geology and soils	Vertic black ultramafic clays which developed from norite and gabbro, also locally in small depressions along streams. Some areas have less clay. Some with high base status and eutrophic red soils. Land type Ea.

Important taxa	**Trees**: *Vachellia nilotica, V. tortilis* subsp. *heteracantha, Senegalia erubescens, S. fleckii, S. mellifera* subsp. *detinens, Combretum imberbe, Searsia lancea, Ziziphus mucronata, Vachellia hebeclada* subsp. *hebeclada, Combretum hereroense, Diospyros lycioides* subsp. *lycioides, Euclea undulata, Grewia flava, Tarchonanthus camphoratus*. **Grasses**: *Aristida bipartita, Bothriochloa insculpta, Digitaria eriantha* subsp. *eriantha, Ischaemum afrum, Panicum maximum, Cymbopogon pospischilii, Eragrostis curvula, Sehima galpinii, Setaria incrassata*. **Shrubs**: *Vachellia tenuispina, Abutilon austro-africanum, Aptosimum elongatum, Hirpicium bechuanense, Pavonia burchellii, Solanum delagoense, Kalanchoe rotundifolia, Talinum caffrum, Heliotropium ciliatum, Kohautia caespitosa* subsp. *brachyloba*.
Remarks	Contains some very clayey soils that swell when wet and shrink when dry. On the clays, woody plant biomass is generally low, and productivity of woody plants is usually lower than that of herbaceous plants. These areas with ultramafic soils are, contrary to Sekhukhuneland, low in species diversity and in endemic species. Erosion is very low to low. Main use is extensive cattle grazing.
References	Bosch (1971), Coetzee (1971), Morris (1972), Van der Meulen (1979), Van der Meulen and Westfall (1980), Pauw (1988), Rutherford (1993), Winterbach (1998), Viljoen et al. (2014).

11. SVcb 2 Madikwe Dolomite Bushveld

Distribution	North West and Limpopo provinces, extends along the low dolomite ridge from the international border at Ramotswa in the west via the Rand Van Tweede Poort, Tlhaapitse and Maakane to west of the Crocodile River near Thabazimbi. It is also found on dolomite hills between Assen and Northam.
Altitude	Altitude 950–1 450 m (median 1 150 m).
Vegetation and landscape features	Gentle ridges and low hills up to about 100–150 m above the surrounding plains. Open (plains) to dense (slopes) woodland with tree and shrub layers often not clearly distinct, especially on steeper slopes; they are dominated by deciduous trees, particularly *Combretum apiculatum* and *Kirkia wilmsii* (especially in the east). Herbaceous layer continuous, dominated by grasses.
Geology and soils	Shallow, stony to rocky soils of the Glenrosa and Mispah forms on dolomite. Land type is mainly Fa.
Important taxa	**Trees**: *Combretum apiculatum, Searsia lancea, Searsia leptodictya, Ziziphus mucronata, Sclerocarya birrea, Ozoroa paniculosa*. **Shrubs**: *Vitex zeyheri, Tarchonanthus camphoratus, Grewia flava, Grewia bicolor, Grewia monticola, Ximenia americana*. **Grasses**: *Heteropogon contortus, Enneapogon scoparius, Aristida congesta, Panicum coloratum, P. maximum*. **Forbs**: *Clerodendrum glabrum, Brachystelma gracillimum, Euphorbia perangusta*.
Remarks	Some species distributions are associated with the east–west climatic gradient, for example *Kirkia wilmsii* is restricted to the eastern parts of the unit where it forms large monospecific forests on mountain slopes. These *Kirkia* forests are indicative of dolomite bands in the bedrock, and they do not occur on other geologies. These forest are especially apparent in autumn when their orange autumn foliage stands out from the surrounding landscape. In contrast to the bush encroachment seen on the red clay loams surrounding this unit, the rocky soils of dolomitic origin support a more open canopy structure and are resistant to bush encroachment.
References	Zacharias (1994), Hudak and Wessman (2001), Stalmans and De Wet (2003).

*d = dominant species, see Table 9 in main text.

12. SVcb 3 Zeerust Thornveld

Distribution	NW, extends along the valleys/plains from the Lobatsi River in the west via Zeerust, Groot Marico and Mabaalstad to the flats between the Pilanesberg and western end of the Magaliesberg in the east (including the valley of the lower Selons River).
Altitude	Altitude mainly 1 000–1 250 m.
Vegetation and landscape features	Deciduous, open to dense short thorny woodland, dominated by 'Acacia' species with herbaceous layer of mainly grasses on deep, high base-status and some clay soils on plains and lowlands, also between rocky ridges of Dwarsberg-Swartruggens Mountain Bushveld.
Geology and soils	Gentle catenal sequences from deep, red-yellow, apedal, freely drained with high base-status on upper slopes grading to sodic vertic or melanic clays in valley bottoms. Land type mainly Ae.
Important taxa	**Trees**: *Vachellia nilotica, Vachellia tortilis, Senegalia fleckii, Senegalia galpinii, Senegalia mellifera*. **Shrubs**: *Grewia flava*, *Aloe marlothii*. **Grasses**: *Eragrostis lehmanniana, Panicum maximum* (d), *Aristida congesta, Cymbopogon plurinodis*. **Forbs**: *Agathisanthemum bojeri, Blepharis integrifolius, Chaetacanthus costatus, Chamaecrista absus, Chamaecrista mimosoides, Cleome maculata, Clerodendrum ternatum, Dicoma anomala, Indigofera filipes, Kyphocarpa angustifolia, Limeum viscosum, Lophiocarpus tenuissimus, Sida chrysantha, Stylosanthes fruticosa*.
Remarks	This unit is somewhat more temperate than the Dwaalboom Thornveld that borders it to the north. It occurs in the valleys of the Swartruggens Mountains. The presence of sodic soils at the base of a catena with bare soils adjacent to a wooded streamline with a dense band of *Vachellia tortilis* above is indicative of this vegetation type.
References	Van Wyk (1959), Van der Meulen (1979), Van der Meulen and Westfall (1980), Malan and Van Niekerk (2005).

13. SVcb 4 Dwarsberg-Swartruggens Mountain Bushveld

Distribution	NW, occurs on hills and ridges east of the Lobatsi River through the Zeerust and the Swartruggens areas to Mabeskraal and the Selons River Valley in the east. Also occurs on the parallel ridges of the Dwarsberge from Witkleigat in the west to the hills of the Dwarsberg area in the east.
Altitude	Altitude about 1 000–1 500 m.
Vegetation and landscape features	Rocky low- to medium-high hills and ridges with some steep faces in places. Height above the surrounding plains can reach about 300 m. Mixed bushveld woodland with variable vegetation structure depending on slope, exposure, aspect and local habitat – various combinations of tree and shrub layers often with dense grass layer. Bush clumps also occur.
Geology and soils	Predominately shale and mudstone with stony shallow soils of the Glenrosa and Mispah soil forms. Land type mainly Fb.
Important taxa	**Trees**: *Senegalia caffra, Olea europaea* subsp. *africana, Buddleja saligna, Combretum molle, Dombeya rotundifolia*. **Grasses**: *Loudetia simplex, Schizachyrium sanguineum, Setaria lindenbergiana, Cymbopogon plurinodis, Elionurus muticus, Heteropogon contortus, Melinis nerviglumis, Setaria sphacelata* var. *sphacelata, Themeda triandra, Trachypogon spicatus, Tristachya biseriata*. **Shrubs**: *Vangueria infausta, Nuxia glomerulata, Erythrophysa transvaalensis, Athrixia elata, Pavonia burchellii, Searsia magalismontana* subsp. *magalismontana, Searsia rigida* var. *rigida*.

Remarks	This vegetation has some similarities with the surrounding Gold Reef Mountain Bushveld; however, it is generally drier and warmer than this unit and is associated with shale/mudstone as opposed to quartzite for Gold Reef Mountain Bushveld. This unit extends into Botswana, for example on the hills around Lobatse. Alien species include *Cereus jamacaru* and particularly *Acacia mearnsii* that form extensive thickets especially on the ecotone with the cooler and moister Rand Highveld Grassland vegetation type.
References	Van der Meulen (1979), Zacharias (1994), Bredenkamp (1999), Viljoen et al. (2014).

14. SVcb 5 Pilanesberg Mountain Bushveld

Distribution	NW, hills and mountains immediately north of Sun City and west of Heystekrand (Mankwe District).
Altitude	Altitude about 1 100–1 500 m.
Vegetation and landscape features	Broad-leaved deciduous bushveld with trees and shrubs with wiry grass layer on slopes of rocky mountains and hills, with mountain summits more grassy and valley floors sometimes less woody but the latter may be related to past disturbance.
Geology and soils	The alkaline complex consists of potassium- and sodium-rich, silica-poor rocks, mainly foyaite, lava and tuff with some syenite. Wide range of elements found, particularly rare earth elements and fluorine in the form of CaF_2 (fluorite). Due to the original volcanic actions, subsequent fracturing, emplacement of intrusions, collapse and resurgence of magma and radial emplacement of dykes, a complex geological pattern exists. Pilanesberg is one of the very few large alkaline ring complexes in the world, approximately 1.3 million years old. Soils are shallow, rocky lithosols on the hills and mountains of the Glenrosa and Mispah soil forms, but with deeper, sandy soils on the valley floors. Land type is Ib.
Important taxa	**Trees**: *Combretum apiculatum, Combretum molle, Combretum zeyheri, Strychnos cocculoides, Croton gratissimus, Englerophytum magalismontanum, Searsia leptodictya, Vangueria parvifolia, Diplorhynchus condylocarpon, Elephantorrhiza burkei, Grewia flava, Hibiscus calyphyllus, Mundulea sericea, Steganotaenia araliacea, Vitex rehmannii, Polygala hottentotta, Xerophyta retinervis, Erythrophysa transvaalensis.* **Grasses**: *Chrysopogon serrulatus, Elionurus muticus, Panicum maximum, Enneapogon scoparius, Hyperthelia dissoluta, Panicum deustum.*
Remarks	This unit is a meeting ground for several species of *Grewia*, for example northwestern limits of *G. occidentalis*, southwestern limits of *G. monticola* and *G. hexamita* and southeastern limits of *G. retinervis*. The vegetation of the southern slopes of this unit is similar to that of the southern slopes of the northeastern end of the Magaliesberg (Gold Reef Mountain Bushveld), whereas the northern slopes of the two units have distinct physiognomic differences. The valley floor vegetation is mapped as Central Sandy Bushveld. The Pilanesberg Alkaline Ring Complex is a near circular (diameter 23–27 km) ring dyke complex constituting an intrusive and extrusive massif with the original volcanic caldera completely eroded away leaving a broken ring of hills and low mountains, as well as the eroded intrusions of the core remaining in the form of many hills and low mountains. Valley floors between the hills and mountains tend to be at most 1–2 km wide.
References	Van Wyk (1959).

15. SVcb 6 Marikana Thornveld

Distribution	North West and Gauteng provinces, occurs on plains from the Rustenburg area in the west, through Marikana and Brits to the Pretoria area in the east.
Altitude	Altitude about 1 050–1 450 m.
Vegetation and landscape features	Open, grassy 'Acacia' woodland occurring on gently undulating plains.
Geology and soils	Most of the area is underlain by the mafic intrusive rocks of the Bushveld Igneous Complex which give rise to heavy black cotton soils (vertic melanic clays). Land type Ea.
Important taxa	**Trees**: *Vachellia karroo, Vachellia tortilis, Vachellia nilotica, Ziziphus mucronata*. **Shrubs**: *Diospyros lycioides, Grewia flava*. **Grasses**: *Aristida bipartita, Bothriochloa insculpta, Digitaria eriantha, Ischaemum afrum, Panicum maximum, Cymbopogon plurinodis, Eragrostis curvula, Sehima galpinii, Setaria incrassata*. **Forbs**: *Abutilon austro-africanum, Aptosimum depressum, Heliotropium ciliatum, Hibiscus trionum, Hirpicium bechuanense, Nidorella hottentotica, Kalanchoe rotundifolia, Pavonia burchellii, Rhynchosia minima, Solanum panduriforme, Talinum caffrum*.
Remarks	Historically this vegetation unit presented as open grass-covered plains. Today, however, due to bush encroachment most of this unit presents as a dense 'Acacia' woodland. The only examples of the open savanna form of this vegetation unit are to be found in communal areas.
References	Van der Meulen (1979), Van Rooyen (1983, 1984), Panagos et al. (1998), Lamprecht (2010), Lamprecht et al. (2011).

16. SVcb 7 Norite Koppies Bushveld

Distribution	North West and Gauteng provinces on 'The Norite Hills' occurring between Rustenburg and Pretoria, north of the Magaliesberg.
Altitude	Altitude about 1 100–1 350 m.
Vegetation and landscape features	Variable woodland, low, semi-open to closed, up to 5 m tall, consisting of dense deciduous shrubs and trees with very sparse undergrowth on shallow rocky soils, with large areas of rock sheet/boulders not covered by vegetation. Tree and shrub layers are continuous. The stands of this unit are found on norite outcrops and koppies, many occurring as inselbergs above the surrounding plains.
Geology and soils	Gabbro (norite is a type of gabbro) of the Bushveld Igneous Complex that give rise to hills with large rocks and boulders and very shallow lithosols. Soils are well-drained, Glenrosa and Mispah forms. Gabbro is a coarse-grained igneous rock that is relatively low in silica and rich in iron, magnesium and calcium. Such rock is described as mafic. Land type Ib.
Important taxa	**Trees**: *Combretum molle, Croton gratissimus, Ficus abutilifolia, Pappea capensis, Bridelia mollis, Psydrax livida, Volkameria glabra, Combretum apiculatum, Diplorhynchus condylocarpon, Dombeya rotundifolia, Euclea natalensis, Euphorbia cooperi, Ficus glumosa, Lannea discolor, Peltophorum africanum, Sclerocarya birrea, Triaspis glaucophylla*. **Shrubs**: *Grewia flavescens, Pouzolzia mixta, Vitex zeyheri, Jatropha latifolia*. **Grasses**: *Chrysopogon serrulatus, Setaria lindenbergiana*. **Forbs**: *Cyphostemma lanigerum, Helinus integrifolius, Hermannia floribunda, Hibiscus subreniformis, Hibiscus schinzii, Pellaea viridis, Turraea obtusifolia, Urera tenax*.

Remarks	Vegetation patterns on norite koppies are primarily determined by the amount of rockiness and aspect, warmer north-facing slopes and cooler south-facing slopes bearing floristically distinct vegetation. A number of the woody species e.g., species of *Ficus*, are typical chasmophytes, penetrating the rocks with their roots (Van der Meulen 1979). The vegetation unit is transitional between xeric lowland bushveld and mesophyllous woodland in cooler more moist upland areas associated with the Magaliesberg. It may be considered to be a more xeric expression of these upland areas (Van der Meulen 1979). There are no endemic plant species associated with this vegetation unit. The unique character of this vegetation unit is derived from the combination of species (communities) and structure of vegetation due to the unique geological structure of the inselbergs. Mining is primarily in the form of granite quarries on koppies, but also affects surrounding lower-lying areas. Areas close to human settlements are often severely disturbed and many woody species may have been harvested from these areas for fuel or building materials. Weeds, including a number of declared aliens, are more common in these disturbed sites. Erosion is very low to moderate. The granite-like hills and koppies west of Madikwe towards the Botswana border are currently not considered part of this vegetation unit. Given further investigation it is likely that this vegetation unit could extend further to the west.
References	Van der Meulen (1979), Panagos (1996), Lamprecht (2010), Lamprecht et al. (2011).

17. SVcb 8 Moot Plains Bushveld

Distribution	North West and Gauteng provinces, main belt occurs immediately south of the Magaliesberg from the Selons River Valley in the west through Maanhaarrand, filling the valley bottom of the Magalies River, proceeding east of the Hartebeespoort Dam between the Magaliesberg and Daspoort mountain ranges to Pretoria. It also occurs as a narrow belt immediately north of the Magaliesberg from Rustenburg in the west to just east of the Crocodile River in the east; also south of the Swartruggens–Zeerust line.
Altitude	Altitude typically about 1 050–1 450 m.
Vegetation and landscape features	Open to closed, low, often thorny savanna dominated by various species of 'Acacia' in the bottomlands and plains, as well as woodlands of varying height and density on the lower hillsides. Herbaceous layer is dominated by grasses.
Geology and soils	Soils varied, mostly stony with colluvial clay-loam or sand derived from shale (south of the Magaliesberg), norite (north of the Magaliesberg), or quartzite. Catenas are distinctive with red-yellow apedal freely drained, dystrophic sandy soils on the top slope near the base of hills down to eutrophic vertic and melanic clays in the bottom-lands. Land types Ba, Bc and Ea.
Important taxa	**Trees**: *Vachellia nilotica, Vachellia tortilis, Searsia lancea, Terminalia sericea, Buddleja saligna, Euclea undulata, Olea europaea, Grewia occidentalis, Gymnosporia polyacantha, Mystroxylon aethiopicum.* **Grasses**: *Heteropogon contortus, Setaria sphacelata, Themeda triandra, Aristida congesta, Chloris virgata, Cynodon dactylon, Sporobolus nitens, Tragus koelerioides.* **Shrubs**: *Aptosimum elongatum, Felicia fascicularis, Lantana rugosa, Teucrium trifidum, Kalanchoe paniculata, Jasminum breviflorum, Listia bainesii, Achyropsis avicularis, Evolvulus alsinoides, Helichrysum nudifolium, Hermannia depressa, Osteospermum muricatum, Phyllanthus maderaspatensis.*
Remarks	Plant communities characteristically vary in relation to catena position. Top slope communities on sandy soils are dominated by broad-leaved woodland (e.g., *Terminalia sericea*). These communities are structurally and floristically very similar to the Central Sandy Bushveld vegetation type. Bottomlands are dominated by 'Acacia' woodland communities on clay rich soils. Plant communities here are similar to Zeerust Thornveld or Marikana Thornveld.
References	Coetzee (1975), Van der Meulen (1979).

18. SVcb 9 Gold Reef Mountain Bushveld

Distribution	North West, Gauteng, Free State and Mpumalanga provinces, occurs on the quartzite ridges of the Swartruggens, Magaliesberg, Witwatersrand, Gatsrand, Suikerbosrand, and Vredefort Dome mountain ranges.
Altitude	Altitude 1 200–1 750 m.
Vegetation and landscape features	Quartzite rocky hills and ridges mostly dominated by wiry, sour grasses on summits with more woody vegetation on slopes associated with distinct floristic differences (e.g., preponderance of *Senegalia caffra* on the southern slopes, *Protea* 'savannas' above 1600 m on southern aspects). Tree cover is variable dependent on soil depth, aspect and rockiness. Tree and shrub layers are often continuous. Herbaceous layer is dominated by grasses. A heterogenous vegetation type with several distinct plant communities discernible based on aspect, slope and rockiness.
Geology and soils	Quartzite bedrock that gives rise to shallow, dystrophic, gravelly lithosols of the Mispah form. Land types mainly Ib and Fb.
Important taxa	**Trees**: *Senegalia caffra, Combretum molle, Protea caffra, Celtis africana, Dombeya rotundifolia, Englerophytum magalismontanum, Ochna pretoriensis, Searsia leptodictya, Vangueria infausta, Vangueria parvifolia, Ziziphus mucronata, Afrocanthium gilfillanii, Ehretia rigida, Grewia occidentalis, Gymnosporia buxifolia, Mystroxylon aethiopicum*. **Grasses**: *Loudetia simplex, Panicum natalense, Schizachyrium sanguineum, Trachypogon spicatus, Alloteropsis semialata, Bewsia biflora, Digitaria tricholaenoides, Diheteropogon amplectens, Sporobolus pectinatus, Tristachya biseriata, Tristachya leucothrix*. **Shrubs**: *Athrixia elata, Pearsonia cajanifolia, Searsia magalismontana, Searsia rigida, Ancylobothrys capensis*. **Herbs**: *Helichrysum nudifolium, Helichrysum rugulosum, Pentanisia angustifolia, Senecio venosus, Xerophyta equisetoides, Cheilanthes contracta, Hypoxis hemerocallidea, Pellaea calomelanos*.
Remarks	This is a very widespread vegetation type stretching across four provinces; however, the dominant species and general physiognomic characteristics of the vegetation type are consistent across its range. All endemic and/or rare plant species in the region are associated with this vegetation type (e.g., *Aloe peglerae, Frithia pulchra, Euphorbia knobelii, Burmannia madagascariensis, Myrsine pillansii, Nuxia glomerulata*). It therefore deserves a disproportionally higher conservation importance value than other vegetation types. This vegetation type is regarded as the 'typical' or 'climax' Bankenveld vegetation type. Many small quartzite ridges that are present in this unit have not been mapped. In addition, some quartzite ridges in Gauteng are currently incorrectly mapped in the National Vegetation Map as Andesite Mountain Bushveld (e.g., Bronberg).
References	Van Vuuren and Van der Schijff (1970), Bredenkamp (1975), Coetzee (1975), Bredenkamp (1977), Bredenkamp and Theron (1978), Behr and Bredenkamp (1988), Bezuidenhout et al. (1988), Du Preez and Venter (1990b) Coetzee et al. (1993), Bezuidenhout et al. (1994c), Coetzee et al. (1994, 1995), Grobler et al. (2002), Pfab (2002), Reddy et al. (2001, 2012), Bredenkamp and Brown (2003a).

19. SVcb 10 Gauteng Shale Mountain Bushveld

Distribution	Gauteng and North West provinces, Occurs on shale and mudstone ridges and hills throughout Gauteng and into eastern NW, notably, the Gatsrand south of Carletonville–Westonaria–Lenasia, and Moot area of the Magaliesberg between Pretoria and Tarlton, and south of Koster.
Altitude	Altitude 1 300–1 750 m.
Vegetation and landscape features	Low, broken ridges varying in steepness and with high surface rock cover. Vegetation is a short (3–6 m tall), semi-open woody thicket or woodland.

Geology and soils	Mostly shale and mudstone that give rise to shallow, rocky lithosols of the Mispah form. Bottom slopes can have deeper rocky, colluvial soils. Land type Fb.
Important taxa	**Trees**: *Senegalia caffra, Dombeya rotundifolia, Vachellia karroo, Celtis africana, Combretum molle, Cussonia spicata, Englerophytum magalismontanum, Protea caffra, Searsia leptodictya, Vangueria infausta, Zanthoxylum capense, Ziziphus mucronata, Asparagus laricinus, Afrocanthium gilfillanii, Osteospermum incanum, Dichrostachys cinerea, Diospyros austroafricana, Diospyros lycioides, Ehretia rigida, Euclea crispa, Grewia occidentalis, Gymnosporia polyacantha, Olea europaea, Tephrosia capensis, Tephrosia longipes.* **Grasses**: *Hyparrhenia dregeana, Cymbopogon caesius, Cymbopogon pospischilii, Digitaria eriantha, Eragrostis curvula.* **Shrubs**: *Acalypha angustata, Asparagus suaveolens, Athrixia elata, Felicia muricata, Indigofera comosa, Searsia magalismontana, Elephantorrhiza burkei, Kalanchoe neglecta, Ancylobothrys capensis.* **Herbs**: *Macledium zeyheri, Helichrysum nudifolium, Helichrysum rugulosum, Hermannia lancifolia, Hibiscus pusillus, Selaginella dregei, Senecio venosus, Hilliardiella aristata, Hilliardiella elaeagnoides, Cheilanthes contracta, Scadoxus puniceus.*
Remarks	This vegetation type is floristically and structurally similar to Andesite Mountain Bushveld with geology as a key differentiating variable. Gauteng Shale Mountain Bushveld is associated with sedimentary shale and mudstone of sedimentary origin, whereas Andesite Mountain Bushveld is associated with andesite rocks of volcanic origin. The vegetation structure and composition of Gauteng Shale Mountain Bushveld together with Andesite Mountain Bushveld and Gold Reef Mountain Bushveld typify the Bankenveld vegetation concept.
References	Coetzee (1972, 1974), Scogings and Theron (1990), Bezuidenhout et al. (1994c, 1994e), Bredenkamp and Brown (2003a).

20. SVcb 11 Andesite Mountain Bushveld

Distribution	Gauteng, North West, Mpumalanga and Free State provinces, Andesite and related igneous rocky ridges and koppies through the region.
Altitude	Altitude about 1 350–1 800 m.
Vegetation and landscape features	Dense, medium-tall thorny mixed bushveld with a well-developed grass layer on hill slopes.
Geology and soils	Andesite volcanic rock that gives rise to shallow, rocky, clayey soils of mainly Mispah and Glenrosa soil forms. Land types Ib and Fb.
Important taxa	**Trees**: *Senegalia caffra, Vachellia karroo, Celtis africana, Protea caffra, Zanthoxylum capense, Ziziphus mucronata, Euclea crispa, Searsia pyroides, Diospyros lycioides, Gymnosporia polyacantha, Lippia javanica, Rhamnus prinoides.* **Grasses**: *Eragrostis curvula, Hyparrhenia finitima, Setaria sphacelata, Themeda triandra, Cymbopogon pospischilii, Digitaria eriantha, Elionurus muticus, Eragrostis racemosa, Eragrostis superba, Panicum maximum.* **Shrubs**: *Asparagus suaveolens, Searsia rigida, Teucrium trifidum, Isoglossa ciliata, Rhoicissus tridentata, Commelina africana, Pseudopegolettia tenella, Aloe davyana.*
Remarks	See remarks for Gauteng Shale Mountain Bushveld.
References	Bredenkamp (1975, 1977), Bredenkamp and Theron (1976, 1978, 1980), Du Preez and Venter (1990a, 1990b), Coetzee et al. (1995), Grobler (2000), Reddy et al. (2001, 2012), Bredenkamp and Brown (2003a), Daemane et al. (2010, 2012).

21. SVcb 12 Central Sandy Bushveld

Distribution	Limpopo, Mpumalanga, Gauteng and North West provinces, on undulating terrain, occurs mainly in a broad arc south of the Springbokvlakte from the Pilanesberg in the west through Hammanskraal and Groblersdal to GaMasemola in the east. A generally narrow irregular band along the northwestern edge of the Springbokvlakte (including Modimolle) extending into a series of valleys and lower-altitude areas within the Waterberg including the upper Mokolo River Valley near Vaalwater, the corridor between Rankins Pass and the Doorndraai Dam, and the lowlands from the Mabula area to south of the Hoekberge. Some isolated sandy patches found on the Springbokvlakte are assigned to Western Sandy Bushveld.
Altitude	Ranges from 900–1 450 m (median 1 070 m).
Vegetation and landscape features	Closed to open broad-leaved woodland with grass-dominated herbaceous layer, relatively low basal cover on dystrophic sands. Undulating plains and valleys, sometimes between mountains, with distinct catenas supporting tall, deciduous *Terminalia sericea* and *Burkea africana* woodland on deep sandy soils (with the former often dominant on the lower slopes of sandy catenas) and low, broad-leaved *Combretum* woodland on shallow rocky or gravelly soils. Species of *Vachellia*, *Ziziphus* and *Euclea* are found on flats and lower slopes on eutrophic sands and some less sandy soils.
Geology and soils	Fersiallitic soils - medium sandy clay loams with good drainage, derived from mafic (basic) granite rocks of the Bushveld Igneous Complex. Undulating landscapes with pronounced catenas. Fa and Fb land types with coarse textured sandy soils. Average depth 0.45 m. Average clay 10%. Well-drained, deep Hutton or Clovelly soils often with a catenary sequence from Hutton at the top to Clovelly on the lower slopes; shallow, skeletal Glenrosa soils also occur.
Important taxa	**Trees**: *Burkea africana, Combretum apiculatum, Combretum zeyheri, Terminalia sericea, Combretum imberbe, Peltophorum africanum, Sclerocarya birrea, Ochna pulchra*. **Grasses**: *Brachiaria nigropedata, Eragrostis pallens, E. rigidior, Panicum maximum, Brachiaria serrata, Elionurus muticus, Eragrostis nindensis, Loudetia simplex, Mosdenia leptostachys, Perotis patens, Themeda triandra, Trachypogon spicatus*. **Herbs**: *Agathisanthemum bojeri, Arthrosolen sericocephalus, Clerodendrum triphyllum, Dicerocaryum zanguebarium, Dichapetalum cymosum, Felicia fascicularis, Indigofera daleoides, Justicia anagalloides, Plexipus hederaceus, Waltheria indica*.
Remarks	*Vachellia sieberiana* occurs in the transition zone with grassland in the east, while *V. caffra* and *Faurea saligna* are dominant in the transition zone to Central Sandy Mountain Bushveld in the western parts of this unit. Central Sandy Bushveld is similar to Western Sandy Bushveld, but the former occurs on aeolian Kalahari sand (often shallow over clay soils) and is generally a taller more open bushveld type. *Vachellia tortilis* and other 'Acacia' species may dominate on heavy clay soil in valleys, but this is assigned to Springbokvlakte Thornveld. This vegetation unit includes probably the most intensively studied South African savanna field site of the South African Savanna Ecosystem Programme in the Nylsvlei Nature Reserve (Limpopo Province). This vegetation type is a complex unit that comprises a variety of distinct vegetation units. In this revision it is proposed that the mountain bushveld vegetation currently included in this unit in the National Vegetation Map is separated out into a new vegetation type (Central Sandy Mountain Bushveld). On the plains, there is also justification for the separation of the *Combretum* woodland on gravelly Glenrosa soils to be separated out from the *Terminalia-Burkea* woodland on deeper sandy Hutton/ Clovelly soils. The former is the dominant type that occurs in the NW, whereas the latter is more dominant in the southern Waterberg where the soils are derived from quartzite rather than granite.
References	Grunow (1965), Coetzee et al. (1976), Van der Meulen (1979), Van der Meulen and Westfall (1980), Lubke et al. (1983), Lubke and Thatcher (1983), Scholes and Walker (1993), Brown (1997), Brown et al. (1995, 1996, 1997), Dörgeloh (1998, 1999a, 1999b), Brown and Bredenkamp (2004).

22. SVcb XX[1] Central Sandy Mountain Bushveld

Distribution	Limpopo, Mpumalanga, Gauteng and North West provinces, Mountainous terrain distributed in a broad arc from the Moretele River northwards into the Waterberg.
Altitude	850–1 450 m (median 1 100 m).
Vegetation and landscape features	Mostly dense broad-leaved mountain bushveld on slopes. Tree layer well-developed consisting of trees taller than three meters with canopy cover of 70–80%. Steep slopes on mountains with mostly skeletal rocky soils, as well as rocky pediments. Includes densely wooded ravines and kloofs that do not contain forest.
Geology and soils	Mostly quartzite of the Rayton Group or coarse-grained granite of the Nebo Granite Group that both give rise to shallow coarse-grained sandy soils with high rock content. Ib land type with shallow rocky soils. Average depth 0.3 m. Average clay 20%.
Important taxa	**Trees**: *Pappea capensis, Combretum apiculatum, Combretum molle, Combretum zeyheri, Bridelia mollis, Gymnosporia glaucophylla, Spirostachys africana, Grewia monticola, Grewia subspathulata, Ochna inermis, Sclerocarya birrea, Lannea discolor, Dombeya rotundifolia, Diplorhynchus condylocarpon* and *Pterocarpus rotundifolius*. Trees such as *Kirkia wilmsii, Croton gratissimus* and *Mimusops zeyheri* are restricted to sheltered ravines. **Grasses**: *Brachiaria deflexa, Aristida canescens, Aristida diffusa, Panicum maximum, Enneapogon scoparius, Chrysopogon serrulatus, Eustachys paspaloides, Digitaria eriantha, Eragrostis rigidior, Melinis repens* and *Enneapogon scoparius*. **Fern**: *Pellaea calomelanos*.
Remarks	See comments for Central Sandy Bushveld. Having been grouped with Central Sandy Bushveld or Western Sandy Bushveld in the National Vegetation Map since 2006 this vegetation type is being reinstated as a vegetation type. It is a well-established vegetation type recognised by Van der Meulen and Westfall (1979); Brown and Bredenkamp (1994); Brown et al. (1995, 1996 and 1997); and Bredenkamp and Brown (2003b). It is synonymous with Van der Meulen's *Combretum molle–Diheteropogon amplectens* Order described in his vegetation map of the western Transvaal bushveld (Van der Meulen & Westfall 1979); Brown's *Pappea capensis–Combretum apiculatum* (mountain) bushveld vegetation type described for the vegetation study of the Borakalalo Nature Reserve (Brown & Bredenkamp 1994, Brown et al. 1995, 1996 and 1997); and Bredenkamp and Brown (2003b) Mogosane Mountain Bushveld and Central Mixed Bushveld vegetation types in their vegetation map of the NW. Note that to the north and the southeast this unit transitions into related mountain bushveld units, namely, Waterberg Mountain Bushveld and Loskop Mountain Bushveld, respectively.
References	Van der Meulen and Westfall (1979), Bredenkamp and Brown (2003b), Brown and Bredenkamp (1994), Brown et al. (1995, 1996, 1997).

23. SVcb 15 Springbokvlakte Thornveld

Distribution	Limpopo, Mpumalanga, North West and Gauteng provinces, flats from Zebediela in the northeast to Hammanskraal and Assen in the southwest, as well as from Bela-Bela and Mookgophong in the northwest to Marble Hall and Rust de Winter in the southeast.
Altitude	Altitude about 900–1 200 m.
Vegetation and landscape features	Black cotton soil flats with open to dense, low thorn savanna dominated by 'Acacia' species or open grassland with a very low shrub layer.

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[1] Vegetation type number to be assigned by the National Vegetation Map Committee.

Geology and soils	Vertisols derived from mafic volcanic rocks of the Bushveld Igneous Complex. Land type Ea.
Important taxa	**Trees**: *Vachellia tortilis, Vachellia karroo, Vachellia nilotica, Vachellia tenuispina, Ziziphus mucronata, Dichrostachys cinerea, Grewia flava*. **Grasses**: *Aristida bipartita, Dichanthium annulatum, Ischaemum afrum, Setaria incrassata, Brachiaria eruciformis*. **Herbs**: *Aspilia mossambicensis, Corchorus trilocularis, Hibiscus trionum, Indigastrum parviflorum, Nidorella hottentotica, Orthosiphon suffrutescens, Rhynchosia minima, Isolepis capensis, Mesogramma apiifolium, Kleinia longiflora, Jamesbrittenia micrantha, Ptycholobium plicatum*.
Remarks	The black clay soils of this unit are characterised by pronounced swelling and cracking with wet and dry cycles, considerable soil cracking when dry, a loose soil surface, high calcium carbonate content in the soil and gilgai micro-relief. Consequently, they are referred to as self-mulching soils and few perennial plants are able to tolerate the physical stress of this soil dynamic leading to a vegetation type with considerably lower species diversity than surrounding vegetation types. They are also referred to as black cotton soils as they are highly suitable for the cultivation of cotton and as a consequence have been extensively cleared for cultivation. Environmentally and floristically this unit is very similar to Marikana Thornveld. The open, grassy savanna form of this vegetation type is very rarely encountered anymore due to bush encroachment and habitat loss through cultivation. Some examples are still to be found in communal areas.
References	Galpin (1926), Coetzee et al. (1976), Van der Meulen (1979), Van der Meulen and Westfall (1980), Winterbach (1998).

24. SVcb 16 Western Sandy Bushveld

Distribution	Limpopo and North West provinces, occurs on flats and undulating plains from Assen near the Crocodile River westwards to the Botswana border between the Swartruggens and Dwarsberg mountain ranges. Also, around Thabazimbi northwards to Steenbokpan and west of the Waterberg Mountains.
Altitude	Mostly at altitudes of 900–1 200 m.
Vegetation and landscape features	Tall, open or closed broad-leaved woodland on gently undulating flats with sandy soils. Bottomlands with clay soils, which are dominated by microphyllous 'Acacia' tree species, belong to the Dwaalboom Thornveld vegetation type.
Geology and soils	Kalahari sand. Quaternary surface deposits comprising remnants of a formerly more widespread covering of Kalahari sand that stretched eastwards as far as the Springbokvlakte. The underlying geology is variable but has no influence on the current surface geology of this vegetation unit. Soils are plinthic catenas, eutrophic, red-yellow apedal, freely drained, high base status, Hutton and Clovelly soil forms. Land types mainly Ae.
Important taxa	**Trees**: *Vachellia erioloba, Senegalia nigrescens, Sclerocarya birrea, Combretum apiculatum, Combretum imberbe, Terminalia sericea, Combretum zeyheri, Lannea discolor, Ochna pulchra, Peltophorum africanum, Combretum hereroense, Euclea undulata, Coptosperma supra-axillare, Dichrostachys cinerea, Grewia bicolor, Grewia flava, Grewia monticola*. **Grasses**: *Anthephora pubescens, Digitaria eriantha, Eragrostis pallens, Eragrostis rigidior, Schmidtia pappophoroides, Aristida congesta, Aristida diffusa, Aristida stipitata, Eragrostis superba, Panicum maximum, Perotis patens*.

Important taxa (continued)	**Shrubs**: *Clerodendrum ternatum, Indigofera filipes, Justicia flava*. **Herbs**: *Blepharis integrifolia, Chamaecrista absus, Evolvulus alsinoides, Geigeria burkei, Cyphocarpa angustifolia, Limeum fenestratum, Limeum argute-carinatum, Lophiocarpus tenuissimus, Monsonia angustifolia*.
Remarks	There are many floristic similarities between this vegetation type and Central Sandy Bushveld. The key difference is that this type occurs on relic aeolian Kalahari sands, whereas the latter is associated with coarse sandy-loam soils derived from the underlying granite rocks. This vegetation type also tends to be taller, more open bushveld whereas the latter is shorter and denser. Large specimens of tree species such as *Vachellia erioloba, Sclerocarya birrea* subsp. *caffra, Senegalia erubescens, V. nigrescens* and *Combretum imberbe* are characteristic of this unit whereas these species are absent from Central Sandy Bushveld. On deeper sands *Terminalia sericea* can form tall, dense stands. Rural settlements between the Pilanesberg, Swartruggens and Dwarsberg is often associated with this unit as the surrounding thornveld units on black cotton soils are not suitable for settlement.
References	Bosch (1971), Herbst (1973), Peel (1990), Peel et al. (1991), Brown and Bredenkamp (1994, 2004), Brown et al. (1995, 1996, 1997), Brown (1997), Winterbach (1998), Winterbach et al. (2000), Stalmans and De Wet (2003).

25. SVcb 17 Waterberg Mountain Bushveld

Distribution	Limpopo Province extending into the far northeast of the NW, Waterberg Mountains, including the foothills, escarpment and tablelands south of the line between Lephalale and Marken and north of Bela-Bela and west of Mokopane and with outliers in the southwest such as the Boshofsberge and Vlieëpoortberge near Thabazimbi.
Altitude	Altitude about 1 000–1 600 m and generally at a lower altitude than the Gm 29 Waterberg-Magaliesberg Summit Sourveld.
Vegetation and landscape features	Rugged mountains with vegetation grading from *Faurea saligna–Protea caffra* bushveld on higher slopes (in turn grading into the Waterberg-Magaliesberg Summit Sourveld) through broad-leaved deciduous bushveld (dominated by *Diplorhynchus condylocarpon*) on rocky mid- and foot slopes to *Burkea africana–Terminalia sericea* savanna in the lower-lying valleys, as well as on deeper sands of the plateaus. The grass layer is moderately developed or well developed.
Geology and soils	Mainly sandstone and quartzite rocks that give rise to dystrophic, acidic sandy, loamy to gravelly soil. Glenrosa and Mispah Forms. Land types mainly Ib, Fa and Ad.
Important taxa	**Trees**: *Vachellia karroo, Senegalia caffra, Burkea africana, Combretum apiculatum, Croton gratissimus, Cussonia transvaalensis, Faurea saligna, Heteropyxis natalensis, Ochna pulchra, Protea caffra, Albizia tanganyicensis, Combretum molle, Englerophytum magalismontanum, Ficus burkei, Ficus glumosa, Ochna pretoriensis, Pseudolachnostylis maprouneifolia, Searsia lancea, Terminalia sericea, Vangueria infausta, Vangueria parvifolia, Diplorhynchus condylocarpon, Elephantorrhiza burkei, Combretum moggii, Combretum nelsonii, Dichrostachys cinerea, Euclea crispa, Lasiosiphon kraussianus, Olea capensis, Searsia pyroides, Strychnos pungens, Vitex rehmannii*. **Grasses**: *Loudetia simplex, Schizachyrium sanguineum, Trachypogon spicatus, Brachiaria serrata, Digitaria eriantha, Elionurus muticus, Enneapogon scoparius, Setaria sphacelata, Themeda triandra, Tristachya leucothrix*. **Shrubs**: *Anthospermum rigidum, Barleria affinis, Felicia muricata, Helichrysum kraussii, Protea welwitschii, Searsia rigida, Dichapetalum cymosum, Parinari capensis, Aloe chabaudii, Lopholaena coriifolia, Ancylobothrys capensis, Rhoicissus revoilii*. **Herbs**: *Berkheya insignis, Chamaecrista mimosoides, Geigeria elongata, Hibiscus meyeri, Xerophyta equisetoides, Haemanthus humilis, Hypoxis rigidula*.

Important taxa (continued)	**Biogeographically important taxa**: Northern Sourveld Endemic, *Encephalartos eugene-maraisii, Chorisochora transvaalensis*. **Central Bushveld endemic**, *Erythrophysa transvaalensis, Mosdenia leptostachys*. **Waterberg endemic**, *Grewia rogersii, Vangueria triflora, Oxygonum delagoense*.
Remarks	Carrying capacity of the vegetation for domestic stock animals is low, especially during the dry season (viz, 'sourveld').
References	Coetzee et al. (1981), Westfall (1981), Westfall et al. (1983, 1984), Ben-Shahar (1988), Van Staden (2002), Van Staden and Bredenkamp (2005), Van Staden et al. (2021).

26. SVk 1 Mafikeng Bushveld

Distribution	NW, west of Mafikeng and south of the Botswana border westwards to around Vergeleë, southwards to Piet Plessis and Setlagole.
Altitude	Altitude 1 100–1 400 m.
Vegetation and landscape features	Dense, well developed, tall (> 5 m) woodland with high canopy cover on deep sand.
Geology and soils	Aeolian Kalahari sand of Tertiary to Recent age on flat sandy plains, soils deep (> 1.2 m). Clovelly and Hutton soil forms. Land types Ah and Ai.
Important taxa	**Trees**: *Vachellia erioloba, Terminalia sericea, Ziziphus mucronata, Vachellia luederitzii, Dichrostachys cinerea, Grewia flava, Searsia tenuinervis, Diospyros austroafricana, Ehretia rigida, Rhigozum obovatum, Tarchonanthus camphoratus, Vachellia hebeclada, Grewia retinervis*. **Grasses**: *Anthephora pubescens, Cymbopogon pospischilii, Digitaria eriantha, Eragrostis lehmanniana, Eragrostis pallens, Eragrostis superba, Eragrostis trichophora, Schmidtia pappophoroides, Stipagrostis uniplumis, Aristida congesta, Aristida meridionalis, Aristida mollissima, Aristida stipitata, Brachiaria nigropedata, Digitaria argyrograpta, Melinis repens, Tragus koelerioides, Urochloa panicoides, Panicum kalaharense*. **Shrubs**: *Aptosimum elongatum, Felicia muricata, Lasiosiphon polycephalus, Helichrysum zeyheri, Pomaria burchellii, Lantana rugosa, Talinum arnotii, Elephantorrhiza burkei, Lycium cinereum, Asparagus africanus*. **Herbs**: *Barleria macrostegia, Erlangea misera, Harpagophytum procumbens, Hermannia tomentosa, Hermbstaedtia odorata, Indigofera daleoides, Limeum fenestratum, Nidorella microcephala, Oxygonum delagoense, Senna italica, Ledebouria marginata*.
Remarks	The absence of *Vachellia haematoxylon* (but present in Molopo Bushveld) is characteristic in this vegetation type. In the east near the Molopo River–Harts River interfluve this unit grades into Vryburg thornveld.
References	Smit (2000).

27. SVk 2 Stella Bushveld

Distribution	NW, North of Vryburg around Stella westwards to Louwna and eastwards to about 20 km west of Delareyville, with patches extending toward the Mafikeng area,
Altitude	Altitude 1 250–1 400 m.
Vegetation and landscape features	Flat to gently undulating deep sand-covered plains with open grassy savanna woodland dominated by very large *Searsia lancea* and (less so) *Vachellia erioloba* trees and *Tarchonanthus camphoratus* shrubs.

Geology and soils	Aeolian Kalahari sand with a calcrete layer at depth overlying a variety of geologies. Deep (> 0.4 m), red-yellow apedal, freely drained soils with high base status. Land types Ae and Ag.
Important taxa	**Trees**: *Searsia lancea, Vachellia erioloba, Tarchonanthus camphoratus, Senegalia caffra, Vachellia hebeclada, Vachellia karroo, Dichrostachys cinerea, Grewia flava, Diospyros lycioides, Ehretia rigida, Grewia flava.* **Grasses**: *Cenchrus ciliaris, Cymbopogon pospischilii, Eragrostis rigidior, Panicum coloratum, Themeda triandra, Aristida congesta, Cynodon dactylon, Eragrostis superba, Eragrostis obtusa, Pogonarthria squarrosa, Sporobolus fimbriatus, Tragus koelerioides.* **Shrubs**: *Asparagus laricinus.* **Herbs**: *Chrysocoma ciliata, Hertia pallens, Osteospermum muricatum, Pentzia viridis, Asparagus africanus, Babiana bainesii, Dicoma capensis, Hermannia quartiniana, Hibiscus pusillus, Indigofera alternans, Indigofera daleoides, Lippia scaberrima, Rhynchosia confusa, Schkuhria pinnata, Solanum supinum, Osteospermum scariosum.*
Remarks	This vegetation type represents the ecotone between the Highveld grasslands to the east and Kalahari bushveld to the west, hence on the margins of this vegetation unit it will grade into these neighbouring vegetation types. As the depth of sand decreases and the underlying calcrete becomes exposed then this unit grades into Western Highveld Sandy Grassland. Due to lack of fire, *Tarchonanthus camphoratus* tends to bush encroach leading to a closed bushveld structure. Flax-leaf fleabane (*Erigeron bonariensis*) is an alien invasive annual daisy species that is a major invader in this vegetation type leading to a loss of grassland. This is particularly a problem on commercial farms where veld fires are suppressed.
References	Smit (2000).

28. SVk 3 Schweizer-Reneke Bushveld

Distribution	NW, Schweizer-Reneke area in the east to Amalia in the west and from the farming areas of around Broedersput in the north to Never Mind (Christiana District) in the south.
Altitude	Altitude 1 250–1 400 m.
Vegetation and landscape features	Gently undulating, deep sand covered plains supporting open, tall camelthorn (*Vachellia erioloba*) woodland sometimes with a dense understory of smaller trees comprising *Vachellia karroo, Searsia lancea, Diospyros lycioides, Grewia flava* and *Tarchonanthus camphoratus*.
Geology and soils	Aeolian Kalahari sand. Deep (0.9–1.2 m) sandy soils, with Hutton and Clovelly the dominant soil forms. Land type Ah.
Important taxa	**Trees**: *Vachellia erioloba, Vachellia karroo, Searsia lancea, Diospyros lycioides, Grewia flava, Tarchonanthus camphoratus, Diospyros pallens, Ehretia rigida, Gymnosporia buxifolia, Searsia tridactyla.* **Grasses**: *Anthephora pubescens, Digitaria eriantha, Heteropogon contortus, Stipagrostis uniplumis, Themeda triandra, Aristida congesta, Aristida stipitata, Chloris virgata, Eragrostis biflora, Eragrostis rigidior, Eragrostis superba, Eragrostis trichophora, Sporobolus fimbriatus.* **Shrubs**: *Asparagus laricinus, Vachellia hebeclada.* **Herbs**: *Aptosimum elongatum, Chrysocoma ciliata, Lasiosiphon polycephalus, Pentzia viridis, Asparagus africanus, Barleria macrostegia, Hermannia tomentosa, Hibiscus pusillus, Indigofera daleoides, Lippia scaberrima, Osteospermum muricatum, Pollichia campestris, Rhynchosia adenodes, Dipcadi papillatum, Nerine krigei.*

Remarks	Very similar to Stella Bushveld but is distinguished by the dominance of very large camelthorn trees (not a feature of Stella Bushveld where *Searsia lancea* is dominant), deeper sand and absence of calcrete near the surface. Very few examples of this vegetation remain as almost the entire extent of this vegetation type has been lost to cultivation.
References	Smit (2000).

29. SVk 4 Kimberley Thornveld

Distribution	North West, Free State and Northern Cape provinces, Most of the Kimberley, Hartswater, Bloemhof and Hoopstad Districts, as well as substantial parts of the Warrenton, Christiana, Taung, Boshof and to some extent the Barkly West Districts. Also includes pediment areas in the Herbert and Jacobsdal Districts.
Altitude	Altitude 1 050–1 400 m.
Vegetation and landscape features	Gently undulating sand-covered plains. Grassy with irregular to well-developed, short tree layer comprising *Vachellia tortilis*, *Senegalia mellifera, Vachellia karroo, Vachellia erioloba* and *Boscia albitrunca*. Grass layer open with much uncovered soil.
Geology and soils	Gently undulating plains of aeolian Kalahari sand overlying Andesitic lavas (basalt). Shallow (0.3 m) sandy loams (15% clay) of the Hutton soil form on top of calcrete. Land type Ae.
Important taxa	**Trees**: *Vachellia tortilis, Vachellia hebeclada, Vachellia karroo, Senegalia mellifera, Searsia lancea, Vachellia erioloba, Tarchonanthus camphoratus, Searsia tridactyla, Ehretia rigida, Grewia flava*. **Grasses**: *Aristida congesta, Cymbopogon pospischilii, Digitaria eriantha, Enneapogon cenchroides, Enneapogon scoparius, Eragrostis lehmanniana, Eragrostis rigidior, Heteropogon contortus, Themeda triandra*. **Herbs**: *Aloe grandidentata, Barleria macrostegia, Lippia scaberrima*.
Remarks	This vegetation type and Western Highveld Sandy Grassland share the same land type and the latter grades into this vegetation type along the east-west aridity gradient. *Senegalia mellifera* and *Vachellia tortilis* are the primary bush encroaching species in this vegetation type.
References	Bezuidenhout (1994, 1995, 2009), Smit (2000).

30. SVk 6 Schmidtsdrif Thornveld

Distribution	Northern Cape, Free State and North West provinces, foot slopes and mid slopes to the southeast and below the Ghaap Plateau from around Douglas in the southwest via Schmidtsdrif towards Taung in the northeast. A small less typical section is found east of the Ghaap Plateau from Warrenton towards Hertzogville.
Altitude	Altitude 1 000–1 350 m.
Vegetation and landscape features	Alluvial terraces in the valley floor of the Harts River. Mostly a short or tall closed shrubby thornveld dominated by *Senegalia mellifera* and *Vachellia tortilis*.
Geology and soils	Red, clay rich (> 30%) alluvial soils with a diagnostic B horizon. Land type Dc.
Important taxa	**Trees**: *Vachellia tortilis, Senegalia mellifera, Ziziphus mucronata, Grewia flava*.

Important taxa (continued)	**Grasses**: *Aristida meridionalis, Enneapogon cenchroides, Eragrostis lehmanniana, Eragrostis obtusa, Enneapogon desvauxii.* **Herbs**: *Aptosimum albomarginatum, Barleria rigida, Justicia incana, Pentzia incana, Hermannia affinis, Hermannia comosa, Ptycholobium biflorum, Roepera pubescens, Lacomucinaea lineata, Lepidium bonariense, Amaranthus praetermissus, Heliotropium ciliatum, Indigastrum parviflorum, Osteospermum muricatum, Seddera capensis, Stachys hyssopoides.*
Remarks	Due to its very favourable agricultural soils much of this vegetation type has been lost to cultivation, as well as settlements.
References	Gubb (1980), Crowe et al. (1981), Bezuidenhout (1994, 2009), Smit (2000).

31. SVk 7 Ghaap Plateau Vaalbosveld

Distribution	Northern Cape and North West provinces, flat plateau from around Campbell in the south, east of Danielskuil through Reivilo to around Vryburg in the north.
Altitude	Altitude 1 100–1 500 m.
Vegetation and landscape features	Flat, rocky karst plateau mostly open grassland with well-developed shrub layer dominated by *Tarchonanthus camphoratus* and *Vachellia karroo*. Tall (> 5 m), dense bush clumps comprising *Vachellia karroo, Searsia lancea, Olea europaea* and *Ziziphus mucronata* occur on low, linear ridges (termed grikes or kluftkarren, see remarks below) that bisect the karst landscape and can run for many kilometres.
Geology and soils	Limestone pavement overlying dolomite with shallow, rocky soils (0.10–0.25 m) of Mispah and Hutton soil forms. Land type Fc.
Important taxa	**Trees**: *Tarchonanthus camphoratus, Searsia lancea, Vachellia karroo, Vachellia erioloba, Senegalia mellifera, Vachellia tortilis, Boscia albitrunca, Olea europaea, Rhigozum trichotomum, Ziziphus mucronata, Diospyros austroafricana, Diospyros pallens, Ehretia rigida, Euclea crispa, Grewia flava, Gymnosporia buxifolia, Lessertia frutescens, Searsia tridactyla, Vachellia hebeclada.* **Grasses**: *Themeda triandra, Anthephora pubescens, Cenchrus ciliaris, Digitaria eriantha, Enneapogon scoparius, Eragrostis lehmanniana, Schmidtia pappophoroides, Aristida congesta, Aristida diffusa, Cymbopogon pospischilii, Enneapogon cenchroides, Enneapogon desvauxii, Eragrostis echinochloidea, Eragrostis obtusa, Eragrostis rigidior, Eragrostis superba, Fingerhuthia africana, Heteropogon contortus, Sporobolus fimbriatus, Stipagrostis uniplumis, Tragus koelerioides.* **Shrubs**: *Aptosimum elongatum, Chrysocoma ciliata, Helichrysum zeyheri, Hermannia comosa, Lantana rugosa, Leonotis pentadentata, Melolobium lampolobum, Peliostomum junceum, Pentzia globosa, Pentzia viridis, Roepera pubescens, Hertia pallens, Lycium cinereum, Thesium hystrix, Asparagus africanus.* **Herbs**: *Barleria macrostegia, Geigeria filifolia, Geigeria ornativa, Gisekia africana, Helichrysum cerastioides, Heliotropium ciliatum, Hermbstaedtia odorata, Hibiscus marlothianus, Hibiscus pusillus, Jamesbrittenia aurantiaca, Limeum fenestratum, Lippia scaberrima, Selago densiflora, Vahlia capensis, Aloe grandidentata, Pentzia stellata.*
Remarks	The Ghaap Plateau is recognised as part of the Griqualand West Centre of Endemism. Important taxa include (GW = Griqualand West endemic, K = Kalahari endemic, D = Broadly disjunct distribution): *Calobota cuspidosa* GW, *Nuxia gracilis* D, *Blepharis marginata* GW, *Putterlickia saxatilis* GW, *Tarchonanthus obovatus* GW, *Euphorbia patula* GW, *Prepodesma orpenii* GW (endemic genus), *Digitaria polyphylla* GW, *Panicum kalaharense* K, *Corchorus pinnatipartitus* GW, *Helichrysum arenicola* K, *Orbea knobelii* K.

Remarks (continued)	Unlike the Malmani karst geology that is mostly covered by Tertiary deposits, both the Ghaap Plateau and the Morokweng karst landscapes can be described as exposed limestone pavements with a very characteristic karst geological weathering pattern immediately observable in aerial imagery. The weathering of these landscapes give rise to low (< 5 m high) linear ridges that run for many kilometres and at odd angles to one another. These are solution fissures that follow joins or faults in the underlying dolomite and the geological term for these ridges is grikes or kluftkarren. These kluftkarren are characteristically covered in woodland vegetation, and in communal areas settlement is often concentrated on these features to avoid occasional flooding. *Tarchonanthus camphoratus* is a woody encroaching species that can dominate the vegetation in parts of the landscape.
References	Smit (2000), Frisby (2016), Frisby et al. (2019).

32. SVk 8 Kuruman Vaalbosveld

Distribution	North West and Northern Cape provinces, east of Kuruman to Lykso, south of Bendell towards Good Hope.
Altitude	Altitude 1 300–1 500 m.
Vegetation and landscape features	Flat to gently undulating shallow sand-covered plains with open grassy savanna woodland characterised by *Vachellia erioloba, Vachellia karroo, Searsia lancea* and *Ziziphus mucronata*. Shrub layer is poorly developed, with *Grewia flava* and *Tarchonanthus camphoratus* and the grass layer is open, with much bare soil in places.
Geology and soils	Aeolian Kalahari sand overlying dolomites of the Ghaap Plateau. Calcrete layer is present. Soils are shallow (< 0.6 m), red sand with a high base status of the Hutton and Clovelly forms. Land types Ae and Ai.
Important taxa	**Trees**: *Searsia lancea, Vachellia erioloba, Vachellia karroo, Ziziphus mucronata, Tarchonanthus camphoratus, Cadaba aphylla, Diospyros austroafricana, Diospyros lycioides, Grewia flava, Gymnosporia buxifolia.* **Grasses**: *Anthephora pubescens, Aristida meridionalis, Anthephora argentea, Eragrostis lehmanniana, Stipagrostis uniplumis, Aristida stipitata, Cymbopogon caesius, Digitaria eriantha, Fingerhuthia africana, Pogonarthria squarrosa, Schmidtia pappophoroides, Themeda triandra, Tragus koelerioides.* **Shrubs**: *Amphiglossa triflora, Anthospermum rigidum, Helichrysum zeyheri, Elephantorrhiza burkei, Rhynchosia holosericea.* **Herbs**: *Acrotome inflata, Dicoma schinzii, Geigeria ornativa, Heliotropium strigosum, Stachys spathulata, Osteospermum scariosum.*
Remarks	Being a dolomite or karst landscape there are many sinkholes that have been filled-in with aeolian sand. These are called dolines. In the Malmani karst landscape (Carletonville Dolomite Grassland) dolines support Olea Sclerophyllous Forest. In this landscape dolines support conspicuous clumps of *Vachellia erioloba*. Kuruman Vaalbosveld is environmentally, structurally and floristically very similar to Stella Bushveld, and both are closely related to Ghaap Plateau Vaalbosveld. Aridity increases from east to west as one descends off the Ghaap Plateau. Kuruman Vaalbosveld is an arid form of Stella Bushveld, and both these vegetation types are distinguished from Ghaap Plateau Vaalbosveld by the presence of a continuous sand layer with no surface limestone (calcrete) or rockiness. Extensive exposures of calcrete, particularly associated with drainage lines and freshwater springs, belong to the Southern Kalahari Mekgacha vegetation type.
References	Smit (2000).

33. SVk 10 Kuruman Mountain Bushveld

Distribution	Northern Cape and North West provinces, from the Asbestos Mountains southwest and northwest of Griekwastad, along the Kuruman Hills north of Danielskuil, passing west of Kuruman town and re-emerging as isolated hills, i.e., Makhubung and the hills around Pomfret in the north. In the NW includes all mountains and hills west of the Harts River that fall in the Molopo River catchment.
Altitude	Altitude 1 100–1 800 m.
Vegetation and landscape features	Open to dense mixed woodland on rolling, rock hills and koppies with generally gentle to moderate slopes and includes the rocky pediment or apron at the base of hills. Grass layer is well developed.
Geology and soils	Various geologies including sandstone, banded ironstone and basalt (andesite). Soils mostly lithosols on upper slopes with deeper, sandy, rocky soils on lower slopes and pediments. Land types Ib and Fb towards the east.
Important taxa	**Trees**: *Searsia lancea, Senegalia mellifera, Dichrostachys cinerea, Diospyros austroafricana, Euclea crispa, Euclea undulata, Olea europaea, Searsia pyroides, Searsia tridactyla, Vachellia nilotica, Tarchonanthus camphoratus, Tephrosia longipes, Searsia ciliata, Boscia albitrunca*. **Shrubs**: *Amphiglossa triflora, Anthospermum rigidum, Gomphocarpus fruticosus, Helichrysum zeyheri, Lantana rugosa, Wahlenbergia nodosa, Ebracteola wilmaniae, Hertia pallens, Rhynchosia totta.* **Grasses**: *Andropogon chinensis, Andropogon schirensis, Anthephora pubescens, Aristida congesta, Digitaria eriantha, Themeda triandra, Triraphis andropogonoides, Aristida diffusa, Brachiaria nigropedata, Bulbostylis burchellii, Cymbopogon caesius, Diheteropogon amplectens, Elionurus muticus, Eragrostis chloromelas, Eragrostis nindensis, Eustachys paspaloides, Heteropogon contortus, Melinis repens, Schizachyrium sanguineum, Trichoneura grandiglumis.* **Herbs**: *Dicoma anomala, Dicoma schinzii, Geigeria ornativa, Helichrysum cerastioides, Heliotropium strigosum, Hibiscus marlothianus, Kohautia cynanchica, Cyphocarpa angustifolia, Boophone disticha, Pellaea calomelanos.* **Griqualand West endemics**: *Calobota cuspidosa, Justicia puberula, Tarchonanthus obovatus, Euphorbia patula, Digitaria polyphylla, Sutera griquensis, Euphorbia patula.*
Remarks	Many species in this unit are widely distributed to the northeast of the subcontinent and reach their southwestern limit in this unit (e.g., *Andropogon schirensis*). There are distinct floristic differences with the relatively nearby and parallel mountains of Koranna-Langeberg Mountain Bushveld. For example, *Croton gratissimus* is common in the Koranna-Langeberg Mountain Bushveld unit but rare in Kuruman Mountain Bushveld. *Calobota cuspidosa* shows just the reverse distributional pattern between these units. The Harts River is used here as the biogeographic and mapping divide between Andesite Mountain Bushveld (east) and Kuruman Mountain Bushveld (west) vegetation types. There are observable floristic changes in this vegetation unit associated with geology and the east–west rainfall gradient. Tree density decreases westwards with the western mountains being more open and dominated by thorn trees. Further floristic analysis is required to determine where the boundary of these two vegetation types is located. Bush encroachment is a major problem in this vegetation type. Both *Senegalia mellifera* and *Dichrostachys cinerea* can form vast impenetrable thickets such as around Pomfret and Heuningvlei.
References	Smit (2000), Van Wyk and Smith (2001).

34. SVk 11 Molopo Bushveld

Distribution	North West and Northern Cape provinces, in the Molopo area from Bray and Werda in the north on the border with Botswana, southwards through Morokweng and Tosca in the east and Vorstershoop to McCarthy's Rest and Eldorado in the west to Bendell in the south.
Altitude	1 000–1 300 m.

Vegetation and landscape features	Flat to gently undulating sandy plains with open Kalahari woodland to a closed shrubland interspersed with numerous small pans. Grass layer is usually very well developed and open.
Geology and soils	Red aeolian Kalahari sand overlying dorbank. Surface calcrete is not present. Soils are deep (> 1.2 m) and sandy (Hutton and Clovelly soil forms). Land type mainly Ah.
Important taxa	**Trees**: *Vachellia erioloba, Boscia albitrunca, Terminalia sericea, Vachellia luederitzii, Vachellia haematoxylon, Lycium hirsutum, Rhigozum trichotomum, Grewia flava, Lycium villosum, Searsia burchellii, Vachellia hebeclada*. **Grasses**: *Aristida meridionalis, Aristida stipitata, Cenchrus ciliaris, Eragrostis lehmanniana, Anthephora argentea, Megaloprotachne albescens, Panicum kalaharense, Aristida congesta, Eragrostis biflora, Eragrostis pallens, Eragrostis rigidior, Pogonarthria squarrosa, Schmidtia kalahariensis, Schmidtia pappophoroides, Stipagrostis ciliata, Stipagrostis uniplumis*. **Shrubs**: *Aptosimum albomarginatum, Aptosimum marlothii, Eriocephalus ericoides, Justicia divaricata, Justicia incana, Elephantorrhiza burkei, Momordica balsamina*. **Herbs**: *Acanthosicyos naudinianus, Acrotome angustifolia, Acrotome inflata, Dicoma schinzii, Geigeria ornativa, Helichrysum cerastioides, Hermannia tomentosa, Hermbstaedtia fleckii, Limeum arenicolum, Limeum fenestratum, Limeum argute-carinatum, Leobordea platycarpa, Senna italica, Sericorema remotiflora, Tephrosia purpurea, Tribulus terrestris*.
Remarks	An extensive unit with increasing diversity of savanna plant species towards the north and northeast. The abundance of small pans throughout this unit and the sparser woody element separate this unit from Mafikeng Bushveld.
References	Smit (2000).

35. SVk XX[*] Vryburg Thornveld

Distribution	NW, headwaters of the Molopo River catchment below the northern edge of the Ghaap Plateau, stretching in an arc from Ganyesa in the south to Mahikeng in the north. Also associated with the eroding flanks of larger west flowing rivers thus it is encountered as far west as Bray along the Molopo River.
Altitude	1 000–1 420 m (median 1 270 m).
Vegetation and landscape features	Open, tall woodland dominated by very tall *Vachellia erioloba* trees and scattered low *Vachellia hebeclada, Senegalia mellifera* and *Dichrostachys cinerea* thickets. *Terminalia sericea* is present but not characteristic or dominant of this vegetation type.
Geology and soils	Aeolian sand with red-yellow, free-draining, apedal soils with high base status (Clovelly and Hutton forms). Average depth 1.2 m. Average clay 8%. Land type Ah.
Important taxa	**Trees**: *Acacia erioloba* (d*), *A. hebeclada* (d), *A. karroo, A. mellifera* (d), *Terminalia sericea*. **Shrubs**: *Tarchonanthus camphoratus* (d), *Dichrostachys cinerea, Grewia flava, Ehretia rigida, Elephantorrhiza elephantina*. **Grasses**: *Anthephora pubescens* (d), *Aristida meridionalis* (d), *Eragrostis pallens* (d), *E. lehmanniana*(d), *Stipagrostis uniplumis* (d), *Cynodon dactylon, Aristida stipitata, Cymbopogon plurinodis, Digitaria eriantha, Eragrostis trichophora, Schmidtia pappophoroides*. **Forbs**: *Asparagus africanus, Chenopodium album, Erlangea misera, Felicia muricata, Gnidia polycephala, Hermannia tomentosa, Indigofera daleoides, Lantana rugosa, Senna italica, Verbesina encelioides*.

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[2] Vegetation type number to be assigned by the National Vegetation Map Committee.

Remarks	The undulating and eroding character of this landscape with exposed dorbank and calcrete (along streams), as well as the presence of springs and hydromorphic grasslands is definitive of this vegetation type. Most of the broad-leaved woody elements and the dense woodland that characterise the neighbouring Mafikeng Bushveld are absent or much reduced here. Eroding slopes mostly expose dorbank hardpan. Only in drainage lines is calcrete encountered (viz. Southern Kalahari Mekgacha). The numerous springs in this landscape are decanting groundwater from the Ghaap Plateau. Consequently, rural settlement in this vegetation type is very high relative to surrounding Kalahari vegetation types.
References	Smit (2000), Bredenkamp and Brown (2003b).

36. SVk XX[3] Morokweng Thornveld

Distribution	NW, Kalahari region around the town of Morokweng.
Altitude	1 060–1 230 m (median 1 148 m).
Vegetation and landscape features	Mostly flat karst landscape with open to dense, low (1–2 m) thornveld with sparse grass layer dominated by herbs and karroid shrubs.
Geology and soils	Dolomite with shallow rocky sandy soils (Glenrosa or Mispah forms) with extensive surface calcrete/limestone present. Average depth < 0.3 m. Average clay 6%. Land type Fc.
Important taxa	**Trees**: *Senegalia mellifera* (d*), *Vachellia hebeclada* (d), *Boscia albitrunca* (d), *Grewia flava* (d), *Lycium cinereum*, *Vachellia erioloba*. **Grasses**: *Eragrostis lehmanniana* (d), *Tragus racemosus* (d), *Aristida congesta*, *Brachiaria marlothii*, *Enneapogon cenchroides*, *Enneapogon scoparius*, *Stipagrostis uniplumis*. **Shrubs and forbs**: *Acrotome inflata*, *Asparagus africanus*, *Felicia muricata*, *Geigeria ornativa*, *Hermannia modesta*, *Hermannia tomentosa*, *Hermbstaedtia odorata*, *Kyphocarpa angustifolia*, *Limeum viscosum*, *Melhania rehmannii*, *Phyllanthus maderaspatensis*, *Senna italica*, *Sericorema remotiflora*, *Tephrosia purpurea*.
Remarks	This is a new vegetation type that is restricted to the NW. Whilst the geology is similar to that of the Ghaap Plateau, the lower rainfall supports a short arid thornveld as opposed to a grassy open woodland encountered in the more mesic Ghaap Plateau Vaalbosveld. Soil biogenic crusts are very well developed in this vegetation type approaching 'elephant skin' structure/texture.
References	Smit (2000).

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[3] Vegetation type number to be assigned by the National Vegetation Map Committee.

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BOTHALIA – African Biodiversity & Conservation
ISSN: (Online) 2311-9284, (Print) 0006-8241

Comparing the effectiveness of pitfall traps and active sampling methods for ants and spiders in a *Chromolaena odorata* invaded site

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Dates

Submitted: 6 April 2023
Accepted: 13 November 2023
Published: 19 April 2024

How to cite this article:

Lauchande, V.L., Mntambo, S.P., Hlongwane, Z.T. & Munyai, T.C., 2024, 'Comparing the effectiveness of pitfall traps and active sampling methods for collecting ants and spiders in a *Chromolaena odorata* invaded site', *Bothalia* 54, a5. http://dx.doi.org/10.38201/btha.abc.v54.5

Background: Active and passive arthropod sampling techniques have their specific limitations. Pitfall trapping is a commonly used passive sampling method, and bush beating, aerial hand collection above the knee, aerial hand collection below the knee cryptic and non-cryptic are widely used active sampling techniques.

Objective and method: Pitfall traps and four active sampling techniques were used in a *Chromolaena odorata* invaded site to compare the methods used in sampling arthropods in Buffelsdraai Conservancy outside the city of Durban, South Africa.

Results: Pitfall traps were the most efficient and the most effective sampling technique with high species richness for both the ant (78%) and spider (76%) samples. One explanation for these differences could be the longer sampling time for passive sampling compared to active sampling.

Conclusion: Compared to the subjective identification of species by collectors in active techniques, the non-selective capturing of species by pitfall traps improves its efficiency. The fewest taxa and individuals were collected by aerial hand collection techniques but these techniques are recommended to supplement pitfall traps. The combination of methods allows for the adequate sampling of the various strata found in vegetatively complex sites. An investigation into the possible use of canopy techniques in *C. odorata* sites would be beneficial, as it considers the various vegetation strata when sampling for biodiversity.

Keywords: Aerial hand collection techniques; pitfall traps; bush beating; biodiversity; ant; spider; *Chromolaena odorata*.

Introduction

Arthropods are found in all ecosystems on Earth and make up most of the biodiversity. They are known to contribute to ecosystem services and maintain the environment (Maleque et al. 2006). Therefore, the shift in their presence and population may be an efficient indicator of changes in the ecosystem (Ozanne 2005). Their vast abundance hinders the quantification of arthropods and has resulted in the development of various sampling techniques (Lowman et al. 1996). The lack of standardisation has led to numerous interpretations of biodiversity estimations for diverse ecosystems (Moir et al. 2005).

Among arthropods, ants are a well-known keystone taxon, highly diverse, and abundant. Their resilience makes them highly sought after when attempting to assess the biodiversity of many different ecosystems (Groc et al. 2007). Pitfall trapping is generally used when sampling ants, except for more vegetatively complex ecosystems where suitable methods such as the Winkler or Malaise sampling method are recommended (Parr & Chown 2001; Sheikh et al. 2018). In contrast, Majer (1997) recommended conducting both hand collection and pitfall traps to get a more complete estimate of ant diversity within complex ecosystems.

Spiders form a highly diverse predator group that globally impacts many tropical ecosystems' functionalities (Kapoor 2006). The relative ease with which spiders are captured has led to the development and use of various cost-effective sampling methods. The limit to these methods is that they generally concentrate on a specific assemblage of arthropods, resulting in a misrepresentation of the community (Green 1999).

Ozanne (2005) found that using various sampling methods simultaneously ensures a more comprehensive assessment. For example, pitfall traps collect ground and leaf litter-dwelling arthropods, while aerial techniques collect a more diverse range of arthropods from different vegetative strata (Malumbres-Olarte et al. 2017). As these invertebrates are sampled to represent the biodiversity within an ecosystem, conducting assessments on diversity changes in invaded forests is of high importance (Muelelwa et al. 2010), but rarely can experiments be performed in ideal conditions, as time and financial constrictions may compel researchers to use a single sampling method (Parr & Chown 2001).

Many restoration projects are implemented on invaded sites to increase biodiversity levels. Efficient biodiversity assessments need to be conducted to represent the change in diversity caused by these invasive species (Muelelwa et al. 2010). As *Chromolaena odorata* is a widespread invasive plant species in South Africa, investigating the impacts it might have on the biodiversity of the invaded ecosystem is of high priority for many ecological researchers (Rejmánek & Richardson 2013).

A series of sugarcane farms located in Buffelsdraai outside the city of Durban in South Africa, originally a scarp forest, are being restored. This has the potential to restore the overall biodiversity that was previously lost. Many cleared forests in Africa and Asia are vulnerable to invasion by *C. odorata*. Therefore, if not biologically controlled and monitored, it hinders many future restoration projects. Reforestation programmes must be monitored to ensure they are accomplishing their intended goals, which are often to restore biodiversity loss (Kanowski et al. 2008). Consistent monitoring of reforested landscapes gauges the success of restoration long after the restoration has been completed (Gerlach et al. 2013).

Of equal importance is a need to quantify and standardise the various methods used to collect biodiversity data for monitoring the success of these monitoring programmes. For arthropods occurring in complex habitat types like forests or alien plant invaded habitats, various sampling methods are available to estimate their diversity in each ecosystem (Moir et al. 2005). These methods tend to be biased depending on the time spent and the number of traps used for the specific technique and externally biased by factors such as the target species and the sampling environment (McCravy 2018). These methods include both active and passive sampling methods as employed by Muelelwa et al. (2010) and Malumbres-Olarte et al. (2017). Malumbres-Olarte et al. (2017) found that combined methods were necessary to ensure that the spider diversity was adequately represented within a vegetatively complex area such as forests.

The current study, therefore, sampled ants and spiders using active and passive methods in sites invaded by *C. odorata* to test their sampling efficiency within vegetatively complex habitats. This study's objectives were to: (i) determine the difference in ant and spider diversity sampled between passive and active sampling methods; and (ii) determine if the ant and spider composition varies between sampling methods. This study hypothesised a difference in diversity and assemblage composition for ants and spiders sampled using techniques employed. We further predicted that active sampling would have a lower species diversity than passive sampling because the longer sampling time increased the capturing potential. We also predicted that there will be a unique assemblage composition associated with active sampling techniques. And lastly, that the individual selection of rare species by aerial hand-collection techniques will reduce the similarity in species composition.

Methods and materials

Study area

The study was conducted in the Buffelsdraai Conservancy (29°37′50.17188″ S, 30°59′0.77352″ E), approximately 25 km north of Durban in KwaZulu-Natal, South Africa. Historically a forested area, 750 ha of the conservancy was cleared for sugarcane production over a 100 years ago. The cultivation of sugarcane was then halted and cleared in 2008, to enforce the Buffelsdraai Landfill Site Community Reforestation Project initiated by the eThekwini Municipality. The primary reason for this was initially to offset the excessive emission of greenhouse gases during the FIFA 2010 World Cup^{TM} in Durban. Additionally, it will be used to mitigate any carbon emission from the nearby landfill site and encourage surrounding communities to grow indigenous tree seedlings to produce goods and food. The study area is located 200–325 m.a.s.l.; this region is characterised by a hot and wet climate in summer, with a cool and dry winter, receiving precipitation of approximately 766 mm in summer, and a mean temperature of 22.2°C in winter to 27.4°C in summer.

The area falls within the KwaZulu-Natal Coastal Belt vegetation type, which is dominated by grasslands and subtropical trees. The cleared sugar cane farm is infested by the invasive species *C. odorata*. The current study was conducted along treatments/habitat types with different gradients of *C. odorata* invasion (high, moderate and none). The gradients of invasion were determined relative to the visible density of *C. odorata* found in the sampling site. High invasion included dense coverage of *C. odorata*, moderate had a scattering of *C. odorata* coverage, and none had no *C. odorata* presence. All these sites/habitats were replicated four times. Also, two habitats representing *C. odorata* cleared and uncleared, each replicated five times, were also sampled.

Ant and spider sampling methods

Most sampling techniques used have been divided into passive and active sampling techniques, depending on the involvement of the collector (Grootaert et al. 2010). The primary passive sampling technique routinely used is pitfall trapping. It involves the focal taxa movements toward the trap (Grootaert et al. 2010; Zou et al. 2012). This cost-effective sampling technique requires less maintenance and eliminates the researcher's subjective bias (Sheikh et al. 2018). In contrast, active sampling methods involve the diligent searching and collecting of arthropods by the researcher, leading to subjective biases (Grootaert et al. 2010; Zou et al. 2012).

Three widely used active techniques are: (i) sweep netting, which involves swinging a net through vegetation, mostly in grassland; (ii) aerial hand collection, which requires the researcher to collect the visible arthropods in each area (Lowman et al. 1996; Moir et al. 2005); and (iii) vegetative beating, which requires the collection of fallen arthropods with a tray from a shaken tree (Ozanne 2005). These methods tend to collect specific arthropod groups and their suitability varies with ecosystem-type.

Pitfall trapping (passive sampling method)

Pitfall traps are efficient for capturing ground-dwelling ant and spider species. Each sampling grid (2 × 5 grids) had ten plastic pitfall traps (± 56 mm diameter) dug into the ground. In each sampling grid, pitfall traps were 10 m apart (total length of the grid, therefore, equal to 50 m). The pitfall traps were half-filled with propylene glycol, which is not an ant attractant or repellent (Munyai & Foord 2011). The pitfall traps were left open for five days at each site. This duration has previously been proven to avoid both over and under-sampling of ant populations (Munyai & Foord 2015). Ants and spiders found in the traps were separated from other invertebrates and stored in 70% ethanol.

Active search methods

Active search sampling methods for ants and spiders included vegetation beating (BB), aerial hand collection above the knee (AHC), aerial hand collection below the knee cryptic (AHC cryptic) and aerial hand collection below the knee noticeable or non-cryptic (AHC OBV). Since densely vegetative ecosystems obstruct the sampling ability to sweep netting, it is commonly replaced with beating in dense vegetation.

For the active search methods, the 50 m transect was divided into three intervals; 0–25 m, 25– 35 m, and 35–50 m. Specimens collected per interval were stored on one vial half-filled with 70% alcohol. Four people carried out active searches. Each person searched for 15 minutes simultaneously per plot/sampling transect. Similar to Robertson et al. (2011), the same person conducted each active search method to try to standardise collector bias.

Ant and spider identification

Ant specimens were identified either to species level using voucher specimens in the School of Life Science, University of KwaZulu-Natal (UKZN) in Pietermaritzburg campus or to genus level using Fisher and Bolton (2016) and then assigned to morphospecies by the last author. A voucher collection with representative specimens is currently placed at the School of Life Sciences at UKZN and Iziko Museum of Cape Town. A.S. Dippenaar-Schoeman at the Agricultural Research Council (ARC) identified the spider specimens to species levels where possible or otherwise genus and then morphospecies. All specimens are housed at ARC in Pretoria.

Statistical analysis

To analyse the collected data, a constant of one was added to the count abundance to ensure that all zero values are logged and analysed. A one-way ANOVA was used on R (R Core Development Team, 2017) to compare active and passive sampling techniques in sampling ant and spider species. The spider and ant data were log transformed to ensure that the assumption of normality was met. The Welch one-way test was run on the ant species collected to test for the difference between passive and active sampling techniques. An alternative one-way ANOVA was conducted on the spider data as they continued to violate normality after being transformed. The Kruskal-Wallis rank sum test was used to test the difference in spider species collected between passive and active sampling methods.

To determine the differences in arthropod diversity within different sampling methods in the study site, the collected data were analysed using diversity indices Simpson's Diversity Index (D), Shannon-Wiener Diversity Index (H'), and Evenness (J') in R (R Core Development Team 2017).

A coverage estimator was used to assess sample completeness (coverage-based rarefaction extrapolation) described by (Chao & Jost 2012). A sample completeness analysis was conducted using iNEXT (Chao et al. 2016).

Using the analysis of similarity (ANOSIM) from the Primer 6+ software package (Clarke & Green 1988), the difference in ant and spider assemblage found by the active and passive sampling strategies were compared. The Global R generated represents the closeness to the compared assemblages, when the significance value is closer to one there is more of a difference (Clarke & Gorley 2001). To adequately represent this significance, estimation of difference was established, the significance of $R > 0.75$ is clearly separated, $R > 0.5$ partially overlaps but is different, and $R < 0.25$ mostly overlaps (Hamer & Slotow 2017). A Non-metric Multi-Dimensional Scaling (NMDS) was conducted using the Global R-value generated to graphically represent these findings, where points with closer distances have more similar assemblages (Patrick et al. 2012).

Results

Ant and spider composition as sampled by various sampling techniques

The passive and active sampling techniques collected 52 222 ants, representing six subfamilies, 24 genera, and 61 species (Table 1A). The collected samples adequately represented the ant community, as the coverage of the sample size was above 0.96 (Figure 1A, Table 2). Formicinae was the most abundant (90.12%) subfamily within the ant specimens, represented by six genera and 14 species (Table 1A), followed by the three subfamilies, each with an abundance below ten percent (Table 1A). The least abundant subfamily was Dorylinae (0.004%), represented by a single genus *Aenictus* (Table 1).

A total of 851 spiders, representing 32 families, 82 genera and 132 species, were collected using both passive and active sampling techniques (Table 1b). The collected samples were an inadequate representative of the spider community, as the sample size coverage was below 0.5, except for the pitfall trap, which was above 0.97

Table 1. The species abundance of six subfamilies of ants (A) and 32 families of spiders (B) collected by active and passive sampling techniques at Buffelsdraai Conservancy, KwaZulu-Natal, South Africa

A)

Ant subfamily	Number of specimens	%
Formicinae	47060	90.12
Myrmicinae	4919	9.42
Ponerinae	206	0.39
Dolichoderinae	23	0.04
Pseudomyrmecinae	12	0.02
Dorylinae	2	0.004

B)

Spider family	Number of specimens	%
Lycosidae	359	42.30
Gnaphosidae	83	9.99
Salticidae	69	8.11
Zodariidae	52	6.11
Theridiidae	40	4.70
Thomisidae	38	4.47
Liocranidae	36	4.23
Araneidae	27	3.17
Nemesiidae	23	2.70
Oxyopidae	20	2.35
Cheiracanthiidae	15	1.76
Clubionidae	13	1.53
Corinnidae	10	1.18
Palpimanidae	10	1.18
Tetragnathidae	8	0.94
Linyphiidae	8	0.94
Philodromidae	7	0.82
Sparassidae	5	0.59
Scytodidae	5	0.59
Ctenidae	3	0.47
Selenopidae	3	0.35
Pisauridae	2	0.24
Uloboridae	2	0.24
Theraphosidae	2	0.24
Cyatholipidae	1	0.12
Cyrtaucheniidae	1	0.12
Mimetidae	1	0.12
Oonopidae	1	0.12
Pholcidae	1	0.12
Segestriidae	1	0.12
Trachelidae	1	0.12

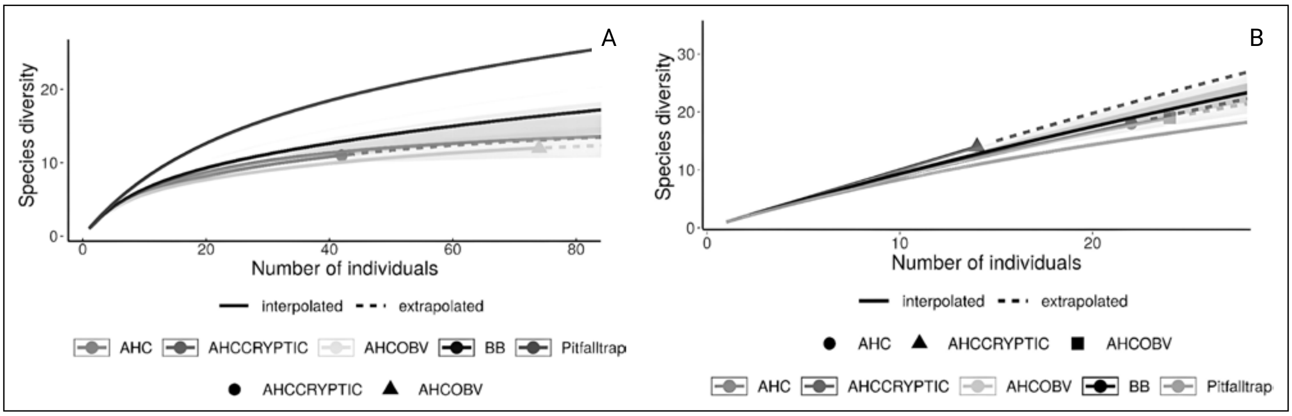

Figure 1. Individual-based rarefaction/extrapolation sampling curves representing ant (A) and spider (B) sampling size collected by both active and passive sampling strategies used at Buffelsdraai Conservancy [AHC = aerial hand collection above the knee; AHCCRYPTIC = aerial hand collection below the knee cryptic; AHCOBV = aerial hand collection below the knee noticeable or non-cryptic; BB = vegetation beating].

(Figure 1B, Table 3). Lycosidae was the most abundant (42.30%) and diverse family with six genera and nine species found (Table 1B). Thirteen families each yielded an abundance of more than one percent (Table 1B).

Seventeen families each yielded an abundance below 1% (Table 1B), of which seven families yielded the lowest abundance (0.12%) and each represented single genera and species (Table 1B). Overall, pitfall trapping was the most successful technique (Table 2 and 3). The sampling technique that collected the fewest individuals of both ants and spiders was aerial hand collection below knee cryptic (Table 2 and 3).

Ant and spider species diversity as sampled by various sampling techniques

Pitfall traps yielded the highest diversity but the lowest variation between taxa (Table 2 and 3). Bush beating was most successful for spiders and sampled the highest diversity (Table 2). Furthermore, pitfall traps yielded the second-highest diversity but the lowest variation for both taxa. For both the ants and spiders, the least diversity but the highest variation in taxa was collected by aerial hand collection below knee cryptic (Table 2 and 3).

There was a significant difference (F-value = 91.72; d.f.n = 4; d.f.d = 51.25; n = 16; Total = 30.956 ± 158.186; $p < 0.0001$) between ant species collected by passive and active sampling techniques. Pitfall traps contributed the highest species richness (39.190 ± 178.320). In comparison, aerial hand collection, below the knee cryptic, contributed the least ant richness (1.405 ± 0.627). The passive sampling technique collected a smaller number of ant species within the *C. odorata* invaded sites (Figure 2).

Within the group, the comparison between AHC and AHC OBV was found to not be significantly different ($p = 0.299$). There was a considerable difference in the means between the rest of the compared sampling

Table 2. The specimen numbers, percentage, morphospecies richness, evenness and sample coverage of the taxonomic groups identified for the ant specimens collected using active and passive sampling techniques. The diversity measure indexes Shannon Wiener (H'), Simpson's (λ), and Pilou evenness (J) calculated for ant species [AHC = aerial hand collection above the knee; AHC CRYPTIC = aerial hand collection below the knee cryptic; AHC OBV = aerial hand collection below the knee noticeable or non-cryptic; BB = vegetation beating]

Sampling techniques	Number of specimens	% of total specimens	Number of families	Number of genera	Number of species	Sampling coverage	Shannon (H')	Simpson's (λ)	Evenness (J)
AHC	184	0.35	5	10	14	0.969	2.218	0.857	0.325
AHC CRYPTIC	59	0.11	4	9	11	0.907	2.001	0.820	0.342
AHC OBV	147	0.28	4	10	12	0.960	2.060	0.845	0.340
BB	296	0.57	4	13	22	0.950	2.423	0.879	0.284
Pitfall trap	51 536	98.69	6	23	56	0.992	3.166	0.941	0.234

Table 3. The specimen numbers, percentage, morphospecies richness and sample coverage of the taxonomic groups identified for the spider specimens collected using active and passive sampling techniques. The diversity measure indexes Shannon Wiener (H'), Simpson's (λ), and Pilou evenness (J) calculated for spider species [AHC = aerial hand collection above the knee; AHC CRYPTIC = aerial hand collection below the knee cryptic; AHC OBV = aerial hand collection below the knee noticeable or non-cryptic; BB = vegetation beating]

Sampling techniques	Number of specimens	% of total specimens	Number of families	Number of genera	Number of Species	Sampling coverage	Shannon (H')	Simpson's (λ)	Evenness (J)
AHC	23	2.70	9	17	18	0.277	2.776	0.926	0.320
AHC CRYPTIC	16	1.88	9	12	14	0	2.639	0.929	0.352
AHC OBV	30	3.53	14	17	19	0.386	2.867	0.938	0.318
BB	121	13.63	14	40	56	0.555	3.938	0.974	0.234
Pitfall trap	666	78.26	27	47	64	0.933	3.628	0.952	0.213

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

techniques, contributing to the variation in richness found as all pitfall comparisons had high significance ($p < 0.0001$). The latter can be inferred that it influenced the different ant species richness (Table 4).

There was a significant difference [H (2) = 57.59, df = 4, mean rank: Pitfall trap = 23.908; BB = 4.681; AHC = 1.545; AHC OBV = 1.091; AHC CRYPTIC = 0.636, Total = (1.255 ± 1.215), $p < 0.0001$], between spider species collected by passive and active sampling techniques. Pitfall traps once again contributed the most spider richness (1.283 ± 1.362). Aerial hand collection, below the knee non-cryptic, contributed the least to spider richness (1.25 ± 0.442). The passive sampling technique collected the highest number of spider species sampled within the *C. odorata* invaded sites (Figure 3).

There was a significant difference between bush beating and aerial hand collection above the knee non-cryptic (Table 5). The latter sampling methods seem to have low to no contribution to the variation in mean richness. Pitfall

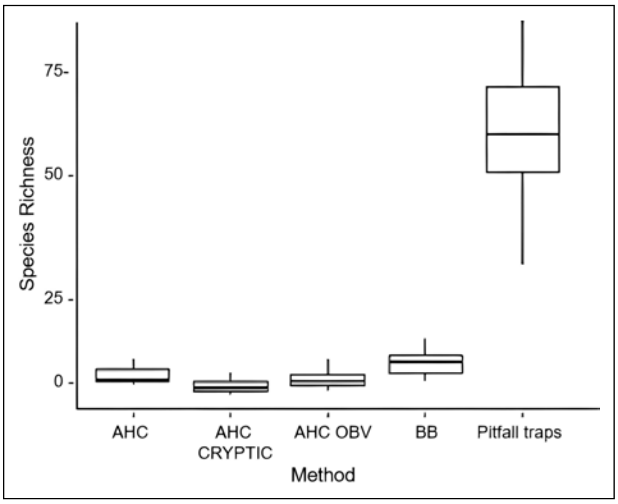

Figure 2. Ant species richness collected using active and passive sampling techniques in Buffelsdraai Conservancy [AHC = aerial hand collection above the knee; AHC CRYPTIC = aerial hand collection below the knee cryptic; AHC OBV = aerial hand collection below the knee noticeable or non-cryptic; BB = vegetation beating].

Table 4. Significance levels from post-hoc comparisons using Turkey (HSD) after two-way ANOVAs were conducted on ant species richness collected with active and passive sampling techniques in Buffelsdraai Conservancy [AHC = aerial hand collection above the knee; AHC CRYPTIC = aerial hand collection below the knee cryptic; AHC OBV = aerial hand collection below the knee noticeable or non-cryptic; BB = vegetation beating]

	AHC	AHC CRYPTIC	AHC OBV	BB	Pitfall trap
Species richness					
AHC					
AHC CRYPTIC	5.9e-6***				
AHC OBV	0.299	0.007**			
BB	0.007**	< 0.0001***	< 0.0001***		
Pitfall trap	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	

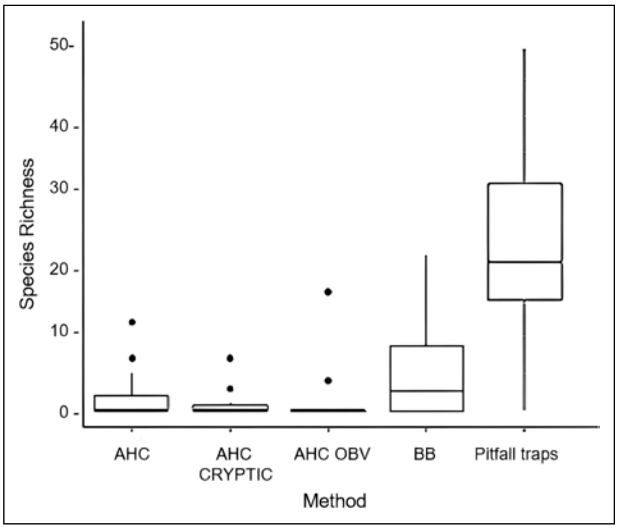

Figure 3. Spider species richness collected using active and passive sampling techniques in Buffelsdraai Conservancy [AHC = aerial hand collection above the knee; AHC CRYPTIC = aerial hand collection below the knee cryptic; AHC OBV = aerial hand collection below the knee noticeable or non-cryptic; BB = vegetation beating].

trap comparisons had high significance (p < 0.0001). Therefore, it was surmised that pitfall traps had the most influence on the differing spider richness (Table 5).

Ant and spider assemblage composition collected by passive and active sampling techniques

The NMDS illustrates a similarity in ant assemblages within passive sampling techniques and similarity within active sampling. Still, there was a distinct separation in ant composition between passive and active sampling techniques (Figure 4A). The ANOSIM also revealed that these are a separated (Global R = 0.945; p = 0.001) assemblage. The NMDS illustrates a similarity in spider's assemblage between sampling techniques, with separation occurring between AHC and AHC CRYPTIC techniques (Figure 4B). The ANOSIM also revealed that there is a partial overlap but a different (Global R = 0.366; p = 0.001) assemblage.

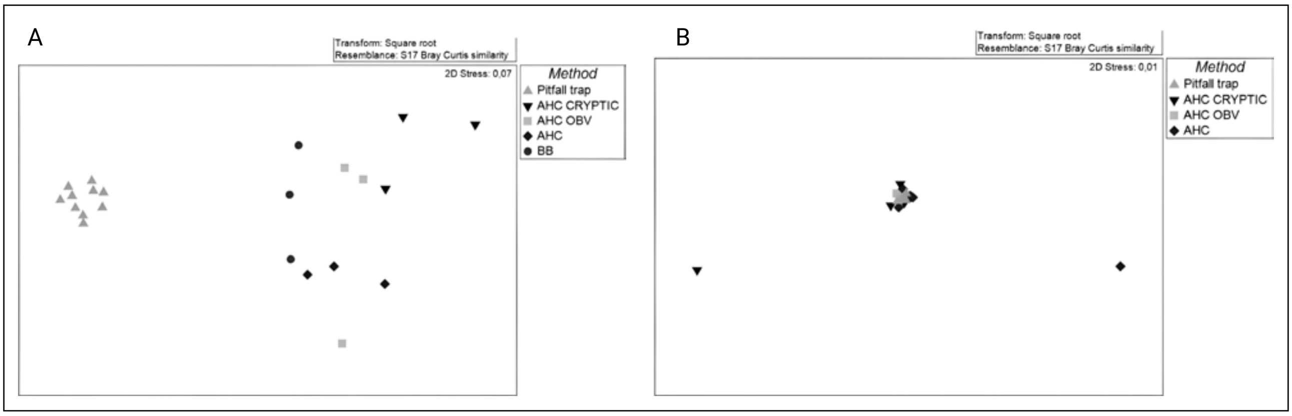

Figure 4. Non-metric Multi-Dimensional Scaling (NMDS) representing the similarity of ant (A) and spider (B) species sampled by active and passive sampling techniques. The count abundance was transformed using square root and the data was analysed using Bray-Curtis similarity to produce a two-dimensional plot with a stress level = 0.07 and = 0.01, respectively [AHC CRYPTIC = aerial hand collection below the knee cryptic; AHC OBV = aerial hand collection below the knee noticeable or non-cryptic; AHC = aerial hand collection above the knee; BB = vegetation beating].

Table 5. Significance levels from post-hoc comparisons using the Dunn test after two-way ANOVAs were conducted on spider species richness collected with active and passive sampling techniques in Buffelsdraai Conservancy [AHC = aerial hand collection above the knee; AHC CRYPTIC = aerial hand collection below the knee cryptic; AHC OBV = aerial hand collection below the knee noticeable or non-cryptic; BB = vegetation beating]

	AHC	AHC CRYPTIC	AHC OBV	BB	Pitfall trap
Species richness					
AHC					
AHC CRYPTIC					
AHC OBV					
BB			0.007**		
Pitfall trap	1.4e-07***	2.0e-09***	4.0e-10***	6.0e-5***	

* = p < 0.05, ** = p < 0.01, *** = p < 0.001

Discussion

In the present study, the ant and spider passive technique samples were comprehensive, with more than 92% sample completeness (Figure 1A and 1B; Table 2 and 3). Therefore, the pitfall trapping is reported as a sampling technique that have represented the sufficient collection of ant and spider diversities found within the sampling site. This is comparable to a study by Muelelwa et al. (2010), who assessed the community of spiders in various woodland, bushveld and forest habitats. The latter study was conducted in the Blouberg Nature Reserve and Western Soutpansberg Conservancy in Limpopo, South Africa. Notably, for ant samples, all active sampling methods were comprehensive with more than 90% of sampling completeness (Table 2). However, spider samples had low sample completeness between 0 and 60% (Table 3). The low percentages suggest that the active techniques data was a poor representation of the site's spider community. However, additional sampling to meet the estimated richness is unfeasible, and the current sampling completeness is then conserved (King & Porter 2005).

In a spider study, Azevedo et al. (2014) argued that low completeness was explained by the high proportion of rare species found in forests, which could be found in the sampled invaded sites. Similar to Cardoso (2009), the expected difference in diversity between passive and active sampling was present, with higher estimated taxonomic diversity in arthropods collected by pitfalls (Table 2 and 3). Within active techniques, the bush beating had the highest estimated diversity compared to hand collection (Table 2 and 3). Tourinho et al. (2018) reported that spiders are generally arboreal and occupy branches of various tree species. Bush beating then dislodges the spider individuals and subsequently, they are collected in the beating sheet. A different study, McCravy (2018), emphasised that bush beating collects a higher proportion of arthropods and that a higher probability of new species is collected.

As expected, the relative distribution (evenness) of spider species was greater in aerial hand collection, cryptic and non-cryptic (Table 3). Whereas the ants higher relative distribution was demonstrated in aerial hand collection below the knee cryptic (Table 2). The abundance of arthropods collected by the aerial hand collection technique is limited in abundance but is methodical in collecting species of specific microhabitats (Sørensen et al. 2002). Like Privet et al. (2020), the individual collection of present arthropods led to a greater variety of species, whether they are mobile, sedentary or hunting, relative to pitfall traps, which were limited to mobile species (Missa et al. 2009). Additionally, the placement of pitfall traps limits the evenness. Pitfall traps located near colony nests increases the collection of individuals from a single species (Grootaert et al. 2010; Sheikh et al. 2018).

Pitfall traps had the highest significant effect on the mean variation of species richness observed (Figure 2 and 3). It also collected higher abundances of species. However, the evenness demonstrates that this abundance is biased toward specific species. They were the most efficient, as this technique collected 78% of the ant species and 76% of the spider species of all methods used in the current study.

The sampling time could have caused the difference between the efficiency of the two techniques. For example, a five-day capture time of pitfall traps allows for the incidental capturing of nocturnal, diurnal and colonising ant and spider species not easily identified by collectors during active sampling (Prasifka et al. 2007). The longer sampling time also helps capture less abundant and less active species (Bali et al. 2019). Moir (2005) reported bush beating as the second most fruitful sampling technique used when sampling ants and spiders (Table 2 and 3). The latter study also observed that bush beating was time efficient but biased against small-bodied taxa.

Like Nsengimana et al. (2017), the current study observed the lowest effect on the mean variation of species richness in aerial hand collection, below the knee cryptic, and non-cryptic active sampling techniques (Figure 2 and 3). The major disadvantages mentioned by several studies are linked to the ant and spider size as larger individuals are easier to identify (Privet et al. 2020).

Additionally, the reduced time limits collecting potential, and the collector's experience restricts the potential for identification, as it is time-consuming and may lead to the collector's fatigue (Berthold et al. 1999; Sørensen et al. 2002; Tuf 2015; Nsengimana et al. 2017). Lastly, active sampling causes a disturbance within the habitat. This disturbance causes an underrepresentation of numbers as many species hide to avoid the collectors (Bali et al. 2019).

Corresponding with Silva et al. (2013), pitfall traps predominately sampled ground-dwelling ants (belonging to the subfamily Formicinae), as this technique is suitable for capturing arthropods actively present in the soil (Table 1A and 2). Pitfalls were also noted to sample a greater number of ant species compared to that of active sampling methods, as the small stature of ants make it harder to identify (Table 2). Similar to Siewers et al. (2014), the current study found that pitfall traps collected a higher number of large-bodied spider species (belonging to the family Lycosidae) compared to small-bodied spider species (belonging to the family Pholcidae) (Table 1b and 3). The difference in size between captured spiders is attributed to the ability of small spiders to escape pitfall traps (Bali et al. 2019). Furthermore, as pitfall traps are frequently used to collect ground-dwelling arthropods, this technique's efficiency in collecting predominately arboreal spiders would be low (McCravy 2018).

The big-bodied epigean spiders (species from the family Lycosidae and Gnaphosidae) were most sampled by pitfall traps (Majer 1997; McCravy 2018; Bali et al. 2019). Based on the NMDS, the ant assemblage indicates a high similarity in ant species collected for each pitfall trap replicate. This assemblage was distinctly separated from active sampling techniques (Figure 4A). As observed, there was a variation within the active sampling techniques. Thayer and Werner (2007) stated that hand collection allows for collecting rare species in microhabitats. However, the success of such sampling will depend on the collector's expertise in identifying potentially rare taxa and the ability to collect them. There was a similar composition between bush beating and aerial hand collection above the knee while aerial hand collection below the knee cryptic and non-cryptic had a similar ant composition. Contrary to this, spider assemblage indicated that mostly all active and passive replicates overlapped with a distinct separation in a single replicate of hand collection above and below cryptic techniques (Figure 4B).

Mgobozi et al. (2008) observed low richness in invaded sites. The current study also reported similar results where low levels of species richness were found for pitfall samples collected in uncleared, high and medium-invaded sites. The likely explanation for the reduction in richness might be the dense vegetation that hindered the trapping of ground-dwelling arthropods. Secondly, plant diversity loss reduced the microhabitats' complexity (Mgobozi et al. 2008; Malumbres-Olarte et al. 2013).

The current study found that pitfall trapping is the most efficient method for sampling ant and spider populations. However, compared to the sampling techniques used, the results present an incomplete representation of ant and spider diversity. The evenness of pitfall traps may be improved by including baiting, as it allows for the collection of individuals from various species attracted to the bait (Sheikh et al. 2018). It would be beneficial to use aerial hand-collection techniques to supplement pitfall traps (Lowman et al. 1996). To improve the study, canopy sampling techniques (for example fogging) must be considered as *C. odorata* grows about six meters tall, encompassing various arboreal species (Malumbres-Olarte et al. 2017).

Conclusion

In conclusion, pitfall traps (as employed here) collected more arthropods from more taxa than either beating or sweep-netting within the *C. odorata* invaded sites of the Buffelsdraai Conservancy. This is likely partly due to the longer time pitfall traps were deployed for compared to the time allowed for the active sampling conducted by the collectors. However, all the sampling techniques have biases. Pitfall traps captured various arthropods while the active sampling techniques were biased toward large-bodied and actively-hunting arthropods. Furthermore, the relative disturbance caused by active sampling reduces the collecting potential and reduces efficiency.

Consequently, biodiversity assessment studies should employ both pitfall traps and active sampling techniques. Specifically, a combination of pitfall traps and hand collection is recommended within forested or similar regions and requires canopy sampling to sample biodiversity adequately.

Acknowledgements

Nokubonga Thabethe, Lindiwe Khoza, Nomathamsanqa Mkhize, Concilia Mukanga, Thandeka Mahlobo and Sbongiseni Xolo are thanked for their help in the field. Lastly, thanks to eThekwini Municipality for allowing us to work at their conservancy. Special thanks to Fatima Alli for helping to identify potential sites for sampling and Prof A.S. Dippenaar-Schoeman at the Agricultural Research Council (ARC) for identifying the spiders.

Competing interests

The authors declare that they have no financial or personal relationship(s) that may have inappropriately influenced them in writing this article.

Authors' contributions

T.C.M. (University of KwaZulu-Natal) designed and conceptualised the study; S.P.M. (University of Mpumalanga) and T.C.M. collected the data; T.C.M. led the curation and identification of arthropods. V.L.L. (University of KwaZulu-Natal) analysed and led the writing (as part of her BSc honours dissertation), under the supervision of T.C.M. Z.T.H. (University of KwaZulu-Natal) formatted and presented the first draft of the manuscript. All authors have read and agreed to the published version of the manuscript.

Ethical considerations

Permission to sample ants and spiders in the study site (Buffelsdraai Conservancy) was approved by the Environmental Planning & Climate Protection Department of the eThekwini.

Funding

The Centre for Invasion Biology and South Africa's National Research Foundation Grant number 114416 provided funding.

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BOTHALIA – African Biodiversity & Conservation
ISSN: (Online) 2311-9284, (Print) 0006-8241

The influence of distance from crushed stone mining on surface-active arthropods and soil chemical properties

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Dates
Submitted: 13 December 2022
Accepted: 2 August 2023
Published: 30 November 2023

How to cite this article:
Yekwayo, I. & Mngeni, A., 2023, 'The influence of distance from crushed stone mining on surface-active arthropods and soil chemical properties', *Bothalia* 54, a1. http://dx.doi.org/10.38201/btha.abc.v54.1

Background: Mining of crushed stone for use in construction is among the various anthropogenic activities in the Eastern Cape province in South Africa that alter natural landscapes. However, little is known about the impact of these activities on arthropods and soil chemical properties.

Objectives: We investigated the effect of distance (5, 30, 50 and 70 metres) from the mining sites on species richness, abundance and composition of surface-active arthropods, as well as composition and concentration of soil chemical properties (soil pH, calcium, magnesium, phosphorus and zinc).

Methods: The study was conducted at two mining sites in Nyandeni Local Municipality within the O.R. Tambo District Municipality that were commissioned in 2014. Arthropods were sampled using pitfall traps and thereafter sorted into morphospecies, while an auger was used to collect soil samples. Permutational multivariate analysis was used to compare the composition of the arthropods and soil chemical properties among distances from the mining activities, while arthropod species richness and abundance, as well as concentrations of soil chemical properties, were analysed using the one-way analysis of variance or Kruskal-Wallis test.

Results: Arthropod species richness, abundance and composition were not influenced by distance from mining activities. Although among soil chemical properties, mining activities altered the concentration of zinc only, we found dissimilarities in soil composition between the sampling point at the edge of the mining activities and sampling points that were away from the mining sites.

Conclusion: We found no evidence of the impact of crushed stone mining on surface-active arthropods; however, our study revealed a negative impact of crushed stone mining on soil chemical properties.

Keywords: ants; beetles; spiders; species richness; Ikwezi mining site; Blue Rock mining site.

Introduction

Mining of stone is important because crushed stone is a construction material for building houses, roads and pavements (Adeyi et al. 2019). However, crushed stone mining has been reported to have a negative impact on the environment (Belay et al. 2020; Kalu & Ogbonna 2021; Otaraku et al. 2019; Pal & Mandal 2017). For example, pollution of water bodies by dust from crushed stone mining activities alters the water quality because of increased sedimentation from the suspended dust particles, high pH levels and water colour that looks grey (Pal & Mandal 2017). Reduced water quality affects aquatic biodiversity negatively, with polluted water leading to the mortality of invertebrates, which reduces the available fish food (Thanigaivel et al. 2023). In addition, heavy metals can pollute the water bodies and negatively impact fish (Thanigaivel et al. 2023).

Generally, the negative effects of mining activities on biodiversity are both direct and indirect. Land degradation and vegetation clearing, which lead to biodiversity loss, are two examples of the direct impact (Otaraku et al. 2019; Sonter et al. 2018). Indirect impact may result from the dust produced from crushing stone, affecting plant species that are sensitive to stone dust (Pal & Mandal 2017). Mining has been shown to negatively impact the density and species richness of local woody plant species, which were found to be significantly greater in unmined sites (Belay et al. 2020). The changes in vegetation cover, diversity and richness of plants directly impact animal species that are dependent on vegetation for food and shelter (Elandalew et al. 2018). For example, the abundance and species richness of some arthropods is positively associated with plant-species richness (Blaise et al. 2022; Ebeling et al. 2018). In addition, mining activities can lead to the establishment of invasive alien plant species, which reduce species richness of arthropods (Litt et al. 2014; Sonter et al. 2018).

Habitat fragmentation may lead to unfavourable living conditions for some animals and therefore trigger migration (Sonter et al. 2018). However, migration is only possible for animals with greater dispersal ability but limited in animals with poor dispersal abilities (Angelova et al. 2020). For example, ground-living arthropods occurring in natural forests did not overlap into the adjacent habitats due to their limited dispersal abilities (Perry et al. 2017; Yekwayo et al. 2017). In addition, mining activities alter habitat structure by decreasing the interior habitats, while increasing the edge. Fragmentation of habitats may influence arthropods negatively because edges decrease species richness and abundance of arthropods and also change assemblages unlike the interior habitats (With & Pavuk 2012).

Besides clearing vegetation, mining activities may contaminate the soil by changing the concentration of nutrients (Adewole & Adesina 2011; Wang et al. 2022). In Nigeria, soil samples in the stone mining area had greater concentrations of metals (nickel, chromium, cadmium, lead, copper, zinc and iron) compared to soil samples outside the mining area (Otaraku et al. 2019). Migliorini et al. (2004) recorded a high abundance of the Collembola, Diplura and Protura in soils with high concentrations of lead, while the Symphyla was not recorded in soils contaminated with lead. Therefore, arthropods respond differently to concentrations of metals in the soil. Furthermore, Lock et al. (2003) reported that an increase in zinc concentration in the soil led to a decrease in the abundance and species richness of springtails. Additionally, Reihart et al. (2021) also showed that greater concentration of nutrients may encourage the spread of invasive ant species, such as *Nylanderia fulva*, which was more abundant in calcium-contaminated soils than in soils without calcium. However, a combination of calcium and potassium was reported to decrease abundance of detritivorous arthropods (Reihart et al. 2021).

Alam et al. (1999) indicated that soil in mining areas tends to be acidic, while Anju and Banerjee (2011) reported that soil was either neutral or alkaline in metal mining areas. In stone mining areas, the soil pH was reported to be alkaline compared to areas where no mining took place (Belay et al. 2020). In addition, soil pH levels may influence the concentration of nutrients available in the soil (Alam et al. 1999; Zhao et al. 2011). For instance, Zhao et al. (2011) found that an increase in soil pH led to an increase in the concentration of calcium, magnesium, manganese and zinc, while soil pH correlated negatively with the concentration of phosphorus and nitrogen.

The concentration of nutrients available in the soil may be influenced by certain arthropod taxa, and that may affect plant growth (Almeida et al. 2019; Kaleri et al. 2020; Smit & Van Aarde 2001; Wagner et al. 1997). For example, activity of millipedes led to high concentration of calcium, phosphorus, potassium, carbon and nitrogen compared to soil that had no millipedes (Smit & Van Aarde 2001). However, different nutrients are influenced differently by the activity of ants (Almeida et al. 2019; Wagner et al. 1997). For instance, in nest soils, there were high concentrations of potassium, phosphorus, nitrate and ammonium, while the concentration of calcium and magnesium did not differ between nest soils and soils that are away from ant nests (Wagner et al. 1997). In addition, activity patterns of ants can lead to an increase in the abundance and species richness of plants, this was evident when comparisons were made between soils in close proximity to and those further away from ant nests (Almeida et al. 2019). Furthermore, high concentrations of soil nutrients, such as, calcium, magnesium, phosphorus and potassium were recorded in soils that had dung beetles compared to soils with no dung beetles (Hanafy & El-Sayed 2012; Kaleri et al. 2020).

Understanding how crushed stone mining alters the concentration of nutrients in the soil is important, as changes in soil nutrients may affect surface-active arthropods directly and indirectly. For example, abundance of *Nylanderia fulva* correlates positively with the concentration of soil calcium (Reihart et al. 2021), while Rosa et al. (2019) reported that different families of spiders correlate with different soil chemical properties. For example, spider families, such as the Gnaphosidae, Lycosidae and Salticidae correlated with calcium, magnesium and potassium, while families, such as the Corinnidae, Theridiidae and Zodariidae correlated with aluminium (Rosa et al. 2019). In addition, as a heavy metal, the concentration of zinc has been reported to be higher at the edges of the stone-mining sites than further away from the mining sites (Kalu & Ogbonna 2021; Ogbonna et al. 2011). Excessively high and/or low concentrations of zinc can affect plant growth negatively (Mousavi 2011; Mousavi et al. 2012). Zinc can indicate the availability of other nutrients, since its availability to plants can be affected by other nutrients, such as phosphorus and potassium (Jiang et al. 2018). For example, an increase in the concentration of phosphorus lead to a decrease in the concentration of available zinc (Mousavi et al. 2012). In addition to soil pH, the current study focused on the following soil chemical properties, zinc, phosphorus and magnesium, all of which are essential nutrients for plant growth (Meng et al. 2021; Mousavi 2011; Yan & Hou 2018; White & Broadley 2003). Response of arthropods to mining activities, such as limestone quarries in Czech Republic (Tropek et al. 2010) and gravel mining in Austria (Zulka 2013) has been investigated. However, according to our knowledge there are no records of the effect of crushed stone mining on arthropods in South Africa, in particular the Eastern Cape. Yet crushed stone mining is one of the growing anthropogenic activities that are taking place in the province (Department of Mineral Resources and Energy).

The first objective of this study was to determine if species richness, abundance and composition of surface-active arthropods change with distance from the crushed stone mining activities. We expected greater species richness and abundance at sampling points further away from the mining sites (where there is less disturbance from mining) than in close proximity to the mining site. Additionally, we hypothesised that species composition of arthropods would vary among the distances from the crushed stone mining activities. Our second objective was to determine if the composition and concentration of soil chemical properties (phosphorus, calcium, magnesium, zinc and pH) change with distance from the mining activities. We expected mining activities to increase the concentration of soil chemical properties at the edge of the mining site compared to away from the mining sites. Furthermore, we expected variation in the composition of soil chemical properties among sampling points. Lastly, we established if any of the soil properties correlated with arthropod species richness and abundance. We hypothesise that different soil properties will affect species richness and abundance of arthropods differently.

Materials and methods

Study area and design

The study was conducted in the Nyandeni Local Municipality within the O.R. Tambo District Municipality in Eastern Cape, South Africa (Figure 1). The area is

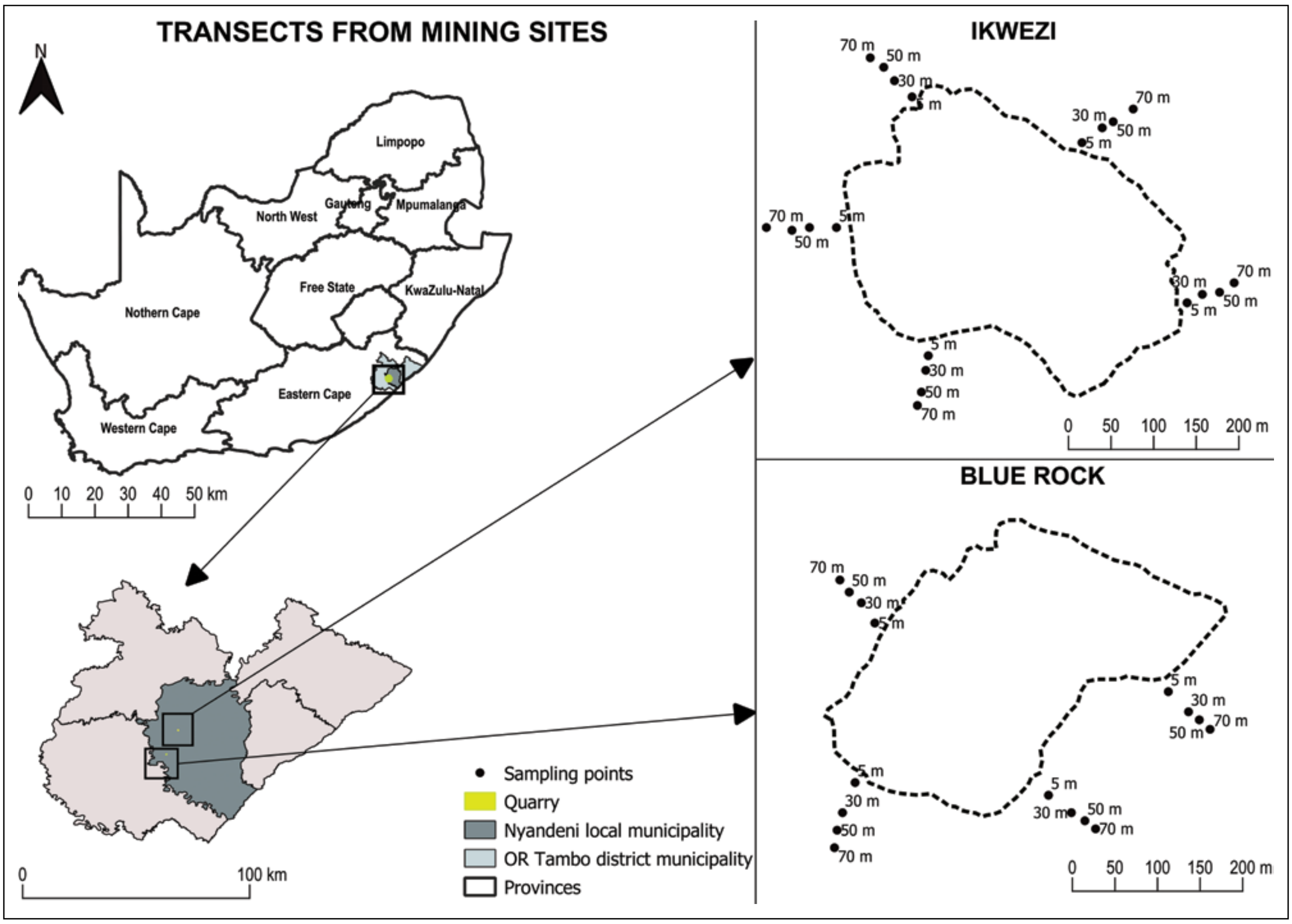

Figure 1. Study sites showing sampling points (5 m, 30 m, 50 m and 70 m) from the mining activities at Blue Rock and Ikwezi mining sites.

characterised by warm (temperatures ranging from 16°C to 28°C) and wet (average monthly precipitation of 64.1 mm) summers, while winters are cool (temperatures ranging from 7°C to 20°C) and dry (Nkamisa et al. 2022). Grassland is one of the dominant biomes in the Eastern Cape. However, the grassland in our study was exposed to various anthropogenic activities, such as conversion into agricultural landscapes (croplands and pastures), mining sites, human settlements, and invasion by alien plant species, such as *Lantana camara*. We investigated two crushed stone mining sites, Ikwezi (-31.529467°, 28.952350°) and Blue Rock (-31.645033°, 28.900633°), which are approximately 13 km apart (Figure 1).

The mining in both sites started in 2014. The active mining at the Ikwezi mining site is approximately 14 ha, while it is approximately 16 ha at the Blue Rock mining site. Although the sizes of these mining sites suggest small scale mining, it is worth noting that the two sites are not the only crushed stone mining sites in the O.R. Tambo District Municipality, thus the importance of studying their effects on arthropods and soil chemical properties. Ikwezi and Blue Rock mining sites occur within a matrix of different anthropogenic activities, including pastures grazed by different livestock (Figure S1). The pastures were the immediate vegetation surrounding the mining sites and were fragmented by roads (footpaths, and gravel and tar roads). In addition to the different grass species in the pastures, there were other plant species, including, aloes, *Berkheya* sp., *Helichrysum* sp., and *Lippia* sp. Furthermore, these pastures were very rocky. Ikwezi mining site was approximately 1 km away from human settlements, unlike the Blue Rock mining site, which was approximately 2 km away from human settlements. However, grazing by livestock occurred in pastures surrounding both mining sites.

Collection and identification of surface-active arthropods

We established nine line transects, five at the Ikwezi and four at the Blue Rock mining sites. Each line transect started from the edge of the mining site (5 m from mining activities) into the surrounding vegetation (pasture). Each transect had four sampling points at 5, 30, 50 and 70 m from the mining activities, and each sampling point was about 1 × 3 m in size. Line transects within the same mining site were ≥ 250 m apart to minimise pseudo-replication. The elevation in the transects ranged from 753−910 m above sea level. Two of these transects were on fairly flat ground, whereas seven were steeper as they got further from the mining sites.

Given that arthropods are known to be active mostly during the warmer months (Mavasa et al. 2022) and have been reported to correlate positively with precipitation (Uhey et al. 2020), we sampled in October 2021. Since the study was focused on surface-active arthropods, the pitfall trapping method was used. Pitfall traps were plastic cups that were 6 cm in diameter and 8 cm deep. According to Samways et al. (2010) traps collect arthropods based on the activity patterns, of which different species may be active at different times of the day and their activity may be influenced by weather patterns. As a result, we sampled arthropods over a period of 28 days. According to Jiménez-Carmona et al. (2019) digging-in effects can be accounted for by opening pitfall traps for ≥ 48 hours, because digging-in effects occur within the first 24 hours after traps have been set out. Therefore, pitfall traps containing 50% of ethylene glycol solution were set out and left open for seven days. Samples were collected from traps on the 7th day, and new traps were set out in the same holes. The process of setting out pitfall traps was repeated four times within 28 days. At each sampling point (5, 30, 50 and 70 m) six pitfall traps that were approximately a metre apart were set out in the shape of a rectangle. Arthropod samples from the six pitfall traps, across all four sampling times at each sampling point, were pooled to form a single sample and preserved in one jar. Specimens were preserved in 70% ethanol before being sorted into morphospecies. Ants were sorted to subfamilies and genus where possible, spiders and beetles were sorted to family level, while cockroaches, millipedes, centipedes, scorpions and pseudoscorpions were identified to order level. Different identification guides were used when sorting specimens (Bouchard 2014; Dippenaar-Schoeman 2014; Dippenaar-Schoeman & Jocqué 1997; Fisher & Bolton 2016; Holm & Dippenaar-Schoeman 2010; Picker et al. 2019; White 1998). The use of morphospecies may lead to over-splitting and lumping of species, however, we used them because Derraik et al. (2002) showed that these limitations only become pronounced when there is a lack of experience with sorting specimens. In our study, the first author, whom has several years of experience, sorted specimens into morphospecies. Voucher specimens are currently housed at the Department of Biological and Environmental Sciences, Walter Sisulu University, however, these voucher specimens will later be housed in the KwaZulu-Natal Museum, Pietermaritzburg.

Collection of soil samples

A total of five soil samples at each sampling point were collected using an auger (8.5 cm in diameter and 14.5 cm deep). The five soil samples were mixed in a bucket to form a sample for each sampling point. We collected soil samples once within the 28 days; however, we acknowledge that it is possible that rainfall, which occurred in some days during this period, may have interfered with available nutrients in the soil surface. Soil samples were stored in Ziploc bags before being sent to the soil analytical laboratory at the Department of Agriculture, Land Reform and Rural Development. The soil chemical properties that were analysed included pH and concentration of phosphorus, calcium, magnesium and zinc.

Data analyses

Although arthropods were collected over four sampling periods, we did not account for repeated sampling in the analyses because samples were pooled immediately after collection from the field and treated as a single sample. Given that the two mining sites were about 13 km apart, we first explored our taxonomic data by testing whether there were differences in species composition of arthropods between the two mining sites. Permutational multivariate analysis of variance (PERMANOVA) in PRIMER 7 was used to compare arthropod assemblages between the mining sites (Anderson 2017). Permutational multivariate analysis of variance showed that the two mining sites support significantly different assemblages of arthropods (PseudoF = 4.78, df = 1, p = 0.0001), indicating that there may be other factors that are unique to each site that are affecting arthropods. As a result, we could not treat transects from the two mining sites as replicates. Instead, we analysed data from each mining site separately. There were five and four line transects at Ikwezi and Blue Rock mining sites respectively.

Given that the pitfall trapping method was used to sample arthropods, we studied incidence data rather than the total abundance data of the sites. As such, the non-parametric estimators (Chao2 and Jackknife2) that are based on incidence data were used to determine whether sampling was sufficient (Chao & Chiu 2016; Hortal et al. 2006). Species richness was estimated in PRIMER 7.

The effect of distance from the mining sites on the composition of arthropods and soil nutrients was determined using PERMANOVA in PRIMER 7. Arthropod data were square-root transformed to reduce the weight of common species, and Bray-Curtis similarity measures with 9999 permutations were used (Anderson et al. 2008). Soil nutrient data were log transformed, normalised and analyses were performed using the Euclidean distance with 9999 permutations (Anderson et al. 2008). Principal coordinates analysis in PRIMER were used to visualise the effect of distance from the mining sites on the composition of soil chemical properties (Anderson et al. 2008).

Species richness and abundance of arthropods, as well as concentrations of soil chemical properties were tested for normality using the Shapiro-Wilk test and the Quantile-Quantile plots in R version 4.1.2 (R Development Core Team 2021). The output of the Shapiro-Wilk test can be affected by the sample size; thus we also used the Quantile-Quantile plots with *ggpubr* package (Kassambara & Kassambara 2020; Rochon et al. 2012). Species richness of arthropods at both mining sites were normally distributed, while the arthropod abundance at both sites were not normally distributed. At Blue Rock mining site, datasets for magnesium and zinc were normally distributed, while datasets for calcium, phosphorus and pH were not normally distributed. At Ikwezi mining site, datasets for soil chemical properties (except for phosphorus) were normally distributed. One-way analysis of variance (ANOVA) compares the means among more than two samples/observations that are normally distributed (Bewick et al. 2004). Therefore, for arthropod and soil nutrient datasets that were normally distributed we used the one-way ANOVA. However, for datasets of arthropods and soil chemical properties that were not normally distributed, we used the non-parametric Kruskal-Wallis test. The Kruskal-Wallis test is a useful statistical tool when examining data that defy normality assumptions, and it is used to compare means of three or more independent groups (Lee 2022). The Tukey multiple comparison post hoc test was used to show differences between paired sampling points (5, 30, 50 and 70 m). Analysis of variance and the Kruskal-Wallis test were performed in R version 4.1.2 (R Development Core Team 2021). Spearman's rank correlations in R version 4.1.2 (R Development Core Team 2021) were used to determine if soil chemical properties correlated with arthropod species richness and abundance.

Results

Number of individuals and morphospecies sampled at Blue Rock mining site

A total of 7 121 individuals in eight arthropod taxa (ants, beetles, spiders, cockroaches, millipedes, centipedes, scorpions and pseudoscorpions) were collected (Table S1). There were 277 morphospecies, of which 51% were singletons and doubletons. There were differences between the observed and estimated species richness (observed = 277, Chao2 = 385.21±26.86, Jacknife2 = 433.63). Out of the three dominant taxa, ants were the most abundant with 5 600 individuals from 46 morphospecies. Collected ants belonged to four subfamilies, with the Myrmicinae and Formicinae being most abundant and species rich, while few individuals and morphospecies were in the Dorylinae, Ponerinae and Dolichoderinae (Table S1). Spiders were represented by 861 individuals and 109 morphospecies. The highest abundance of spiders was in the Lycosidae, Gnaphosidae, Salticidae and Zodariidae (Table S1), whereas the Ammoxenidae, Pholcidae, Pisauridae and Selenopidae were represented by a single individual each (Table S1). The most species-rich families of spiders were the Lycosidae and Salticidae, while many families had a single morphospecies each (Table S1).

Beetles were the least abundant group within the three dominant taxa, with 449 individuals in 91 morphospecies. The most abundant families of beetles were the Staphylinidae, Curculionidae, Scarabaeidae, Tenebrionidae and Carabidae (Table S1). The Histeridae and Nitidulidae had two individuals each, while the Hydrophilidae and Cleridae were represented by a single individual each (Table S1). Beetle families with high numbers of morphospecies were the Staphylinidae, Curculionidae, Scarabaeidae, Chrysomelidae and Carabidae, while the least species-rich families were Hydrophilidae and Cleridae with one morphospecies each (Table S1).

Number of individuals and morphospecies sampled at Ikwezi mining site

There were 9 808 individuals in 292 morphospecies (47% were singletons and doubletons) of ants, beetles, spiders, cockroaches and centipedes collected (Table S1). There were differences between the observed and the estimated species richness (observed = 292, Chao2 = 424.25±33.02, Jacknife2 = 462.12). Out of the three dominant taxa, ants had 5 596 individuals in 40 morphospecies, spiders had 2 132 individuals in 110 morphospecies, while beetles had 1 950 individuals in 109 morphospecies. Ants followed the same patterns as the one at the Blue Rock site, with the Myrmicinae and Formicinae being greater contributors in abundance and species richness, while the opposite was true for the Dorylinae, Ponerinae and Dolichoderinae (Table S1). When it comes to spiders, the Lycosidae, Gnaphosidae and Zodariidae were the most abundant families (Table S1). The highest number of morphospecies were in the Lycosidae and Salticidae, while many families had a single morphospecies (Table S1). The Staphylinidae, Scarabaeidae, Elateridae, Carabidae, Curculionidae, Chrysomelidae and Scydmaenidae had the highest number of individuals of beetles (Table S1). The most species-rich families of beetles were the Staphylinidae, Scarabaeidae, Curculionidae and Carabidae, while other families were represented by six, three, two or one morphospecies (Table S1).

Effect of distance from mining sites on surface-active arthropods and soil chemical properties

Species composition of arthropods was not significantly influenced by distance from the mining sites (both Blue Rock and Ikwezi) (Table 1). Species richness (df = 3, SS = 112.2, MS = 37.40, F = 0.43, p = 0.74) and abundance (χ^2 = 2.63, df = 3, p = 0.45) at Blue Rock did not differ among the sampling points from the mining site. Similarly, distance from Ikwezi mining site did not affect species richness (df = 3, SS = 23, MS = 7.65, F = 0.08, p = 0.97) and abundance (χ^2 = 1.81, df = 3, p = 0.61).

Permutational multivariate analysis of variance showed that the composition of soil chemical properties is significantly influenced by the distance from the mining sites (Table 1). At Blue Rock mining site, the first axis contributed 44.9% of the total variation in composition of soil chemical properties when compared to the second axis, which contributed 25.3% (Figure 2A). The first and second axes contributed 38.2% and 30.8%, respectively, towards variations in the composition of

Table 1. Effect of distance from the mining sites (DMS) on species composition of arthropods and composition of soil chemical properties determined using the permutational multivariate analysis of variance. Significant p-values (p < 0.05) are in bold

	Arthropods		**Soil chemical properties**	
	PseudoF	**p-value**	**PseudoF**	**p-value**
DMS (Blue Rock)	0.71	0.98	2.56	**0.005**
DMS (Ikwezi)	0.93	0.67	2.11	**0.009**
	Pairwise comparisons for soil properties at Blue Rock		**Pairwise comparisons for soil properties at Ikwezi**	
	t-value	**p-value**	**t-value**	**p-value**
5 m and 30 m	0.87	0.51	0.85	0.71
5 m and 50 m	1.91	**0.03**	1.28	0.09
5 m and 70 m	2.04	**0.03**	1.91	**0.008**
30 m and 50 m	1.17	0.26	0.94	0.54
30 m and 70 m	1.61	**0.03**	2.22	**0.008**
50 m and 70 m	1.47	0.06	1.34	0.19

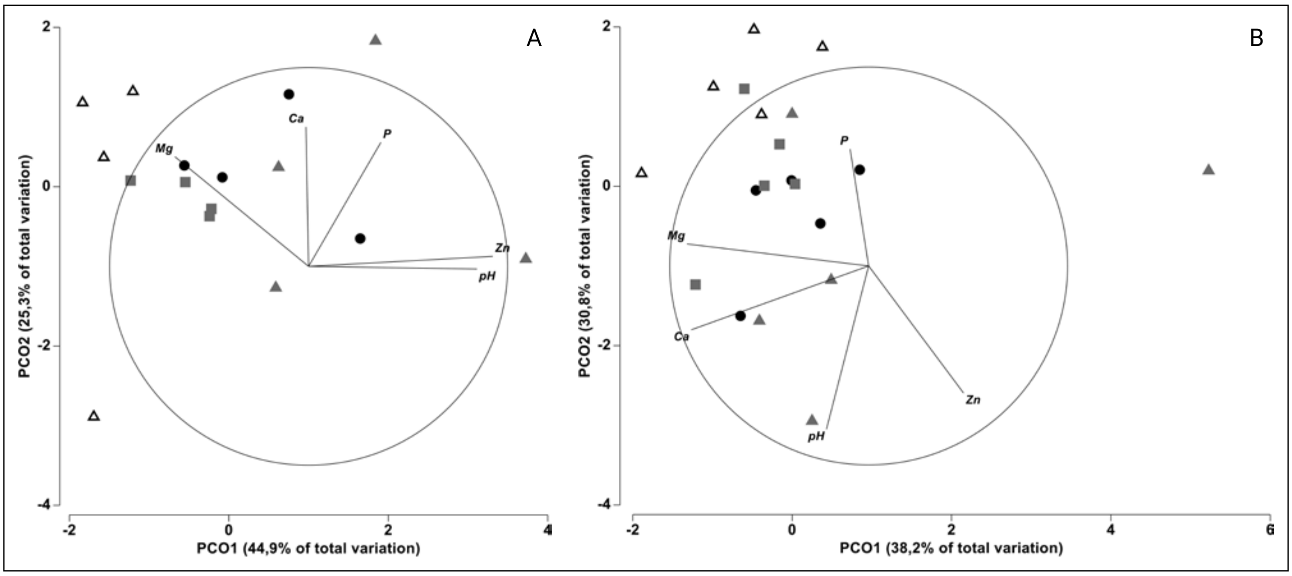

Figure 2. Principal coordinates analyses (PCO) of the composition of soil chemical properties across sampling points from A, Blue Rock and B, Ikwezi mining sites. Grey triangles = 5 m, circles = 30 m, squares = 50 m, and open triangles = 70 m from the mining activities.

soil chemical properties among distances from the Ikwezi mining site (Figure 2B). At Blue Rock mining site, significant differences in soil nutrient composition were detected between the 5 and 50 m sampling points, 5 and 70 m sampling points, as well as between 30 and 70 m sampling points (Table 1, Figure 2A). Sampling points that were in close proximity to each other (5 and 30 m, 30 and 50 m, as well as 50 and 70 m) at Blue Rock mining site did not differ in soil nutrient composition (Table 1, Figure 2A). However, at Ikwezi mining site the soil nutrient composition at the 70 m sampling point was significantly different from the composition at 5 and 30 m sampling points (Table 1, Figure 2B). In contrast, no other pairs showed differences at Ikwezi mining site (Table 1, Figure 2B).

Distance from the mining sites (Blue Rock and Ikwezi) significantly affected the zinc concentration, while other soil chemical properties were not significantly affected (Table 2). The concentration of zinc at Blue Rock

Table 2. Effect of distance from the mining sites (DSM) on concentrations of soil chemical properties that were determined by one-way analysis of variance (ANOVA) and Kruskal-Wallis test. P-values of significant variables ($p < 0.05$) are in bold

		ANOVA				Kruskal-Wallis			
		SS	MS	F-value	p-value			χ^2	p-value
Blue Rock						**Blue Rock**			
Magnesium	DSM	478693	159564	2.66	0.09	Calcium	DSM	3.45	0.33
	Residuals	720541	60045			Phosphorus	DSM	1.56	0.67
Zinc	DSM	31.79	10.59	29.23	**< 0.001**	pH	DSM	6.73	0.08
	Residuals	4.35	0.36						
Ikwezi						**Ikwezi**			
Calcium	DSM	757682	252561	0.14	0.93	Phosphorus	DSM	3.95	0.27
	Residuals	28229040	1764315						
Magnesium	DSM	35013	11671	1.19	0.35				
	Residuals	157244	9828						
Ph	DSM	0.06	0.02	0.40	0.75				
	Residuals	0.76	0.05						
Zinc	DSM	38.02	12.68	55.65	**< 0.001**				
	Residuals	3.64	0.23						

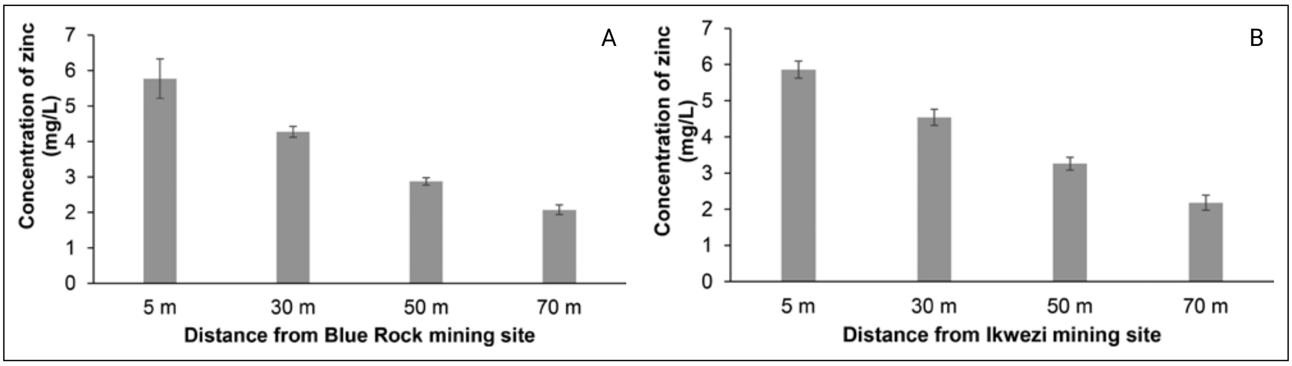

Figure 3. Effect of distance from the mining sites on the mean values of zinc. A, Blue Rock and B, Ikwezi mining site.

mining site differed between 5 and 30 m (p = 0.02), 5 and 50 m (p < 0.001), 5 and 70 m (p < 0.001), 30 and 50 m (p = 0.03), as well as 30 and 70 m (p = 0.001) (Figure 3A). However, the concentration of zinc at Blue Rock mining site did not differ (p = 0.29) between 50 and 70 m sampling points (Figure 3A). At Ikwezi mining site the pairwise comparisons showed significant differences in the concentration of zinc between all paired sampling points, 5 and 30 m (p = 0.002), 5 and 50 m (p < 0.001), 5 and 70 m (p < 0.001), 30 and 50 m (p = 0.003), 30 and 70m (p < 0.001), 50 and 70 m (p = 0.01) (Figure 3B). In both mining sites, greater concentrations of zinc were recorded at 5 m from the mining sites, while the lowest were at 70 m from the mining sites (Figure 3).

Species richness and abundance of arthropods did not correlate with most soil chemical properties (except for calcium and pH) (Table 3). At Blue Rock mining site, a negative correlation (rho = -0.57, p = 0.03) between calcium and arthropod abundance was recorded (Table 3). A positive correlation (rho = 0.54, p = 0.03) between arthropod species richness and soil pH was recorded at Blue Rock mining site (Table 3). Arthropod abundance was negatively correlated with soil pH (rho =-0.48, p = 0.03) at Ikwezi mining site (Table 3).

Table 3. Spearman's rank correlation coefficients (rho) between soil chemical properties, as well as arthropod species richness (SR) and abundance (A). Correlation coefficients and p-values are in bold when significant (p < 0.05)

	Blue Rock mining site		**Ikwezi mining site**	
Soil properties	**rho**	**p-value**	**rho**	**p-value**
Zinc (SR)	0.25	0.35	-0.15	0.52
Zinc (A)	0.15	0.58	-0.22	0.36
Phosphorus (SR)	0.29	0.28	0.11	0.65
Phosphorus (A)	0.49	0.06	-0.12	0.62
Calcium (SR)	-0.47	0.07	-0.14	0.55
Calcium (A)	**-0.57**	**0.03**	-0.42	0.06
Magnesium (SR)	-0.25	0.34	-0.31	0.19
Magnesium (A)	-0.26	0.32	-0.05	0.84
pH (SR)	**0.54**	**0.03**	-0.04	0.86
pH (A)	0.40	0.12	**-0.48**	**0.03**

Discussion

Effect of distance from the crushed stone mining sites on surface-active arthropods

In this study, we expected species richness and abundance of surface-active arthropods to increase with increasing distance from the mining activities, and species composition to change with distance from the mining activities. However, the distance from the mining activities did not affect species richness, abundance or composition. This was surprising considering the fact that crushed stone mining is an anthropogenic activity, of which some anthropogenic activities affect some arthropods negatively. For example, when compared to conserved sites Rivas-Arancibia et al. (2014) reported a decrease in abundance of *Pheidole skwarrae*, *P. tepicana*, *Pogonomyrmex barbatus* and *Dorymyrmex pyramicus* in sites disturbed by livestock grazing, human activities and land degradation. However, abundance of *Brachymymex musculus* increased in disturbed sites compared to undisturbed sites (Rivas-Arancibia et al. 2014). Similarities in species richness, abundance, and composition of surface-active arthropods among the different distances from the mining sites may be because the mining sites that we sampled are like 'islands' that occur within a matrix of other anthropogenic activities. This matrix included pastures that are fragmented by roads and residential areas.

Savage et al. (2018) used the disturbance tolerance hypothesis and reported that arthropods, which occur in disturbed habitats, tend not to be affected by drastic or severe disturbance compared to those occurring in less disturbed habitats. As such, arthropods in our study are probably not affected by crushed stone mining activities because they exist in disturbed areas, and they may have become tolerant of the disturbance. Furthermore, in Denmark, disturbance-adapted species of arthropods led to greater species richness in disturbed habitats compared to undisturbed habitats (Brunbjerg et al. 2015). High arthropod diversity in disturbed habitats may be due to species that are early colonisers of disturbed sites and species that can tolerate disturbance (McCluney & Sabo 2014). McCluney and Sabo (2014) also found greater diversity of carabids (early colonisers) near artificial pools, and greater diversity of wolf spiders in sites that were temporarily dry, indicating their tolerance to habitat changes. The resilience of spiders to habitat change was also evident when Lowe et al. (2017) recorded similarities in abundance among three habitat types (urban parks, remnant vegetation and bushland sites). Therefore, similarities in species richness, abundance and composition of spiders among the four sampling points in our study may be linked to resilience of spiders to habitat change.

Of the arthropods that we collected, the abundant and speciose taxa were ants, spiders and beetles. Given that spiders, some ants and some beetles are predators, they occupy a variety of habitats because they are influenced by the availability of prey. Some ant species are generalist foragers that occupy different habitats (Rivas-Arancibia et al. 2014), this may explain the similarities in species richness, abundance and composition among our sampling points. In addition, two of the most abundant and species-rich families of beetles (ground and rove beetles) are predators, which can occupy diverse habitats. Microhabitats for rove beetles include leaf litter, dung, decaying matter and underneath stones (Picker et al. 2019). In our study, dung from grazing livestock was readily available in the pasture areas. The availability of dung in the pastures that serves as food for dung beetles may have led to their high species richness and abundance in our sampling points (Picker et al. 2019).

The surrounding matrix can potentially influence the density and composition of arthropods in a habitat occurring within that matrix; for example, arthropod density in a grassland surrounded by crop fields (Madeira et al. 2016), and arthropod composition in natural forests surrounded by pine plantations or grassland (Yekwayo et al. 2016). In our study, the influence of the surrounding matrix can be used to explain our results because the crushed stone mining sites are a disturbance occurring in a matrix of pastures. As such, microhabitats within the pastures may have led to high arthropod richness and abundance in our sampling points.

Similarities in species composition of arthropods across our sampling points may also have been due to the short distance among points and the uniformity of vegetation type around the mining sites. Swart et al. (2018) found that assemblages of arthropods in the interior of the natural forest (100 m from the edge) overlapped into the adjacent habitats. However, the extent of overlap was dependant on the type of the adjacent habitat and arthropod taxa (Swart et al. 2018). For example, natural forest assemblages of arachnids overlapped up to 10 m from the edge into the plantation blocks that had been cleared for rehabilitation, while significant differences were observed at 50 m into pine plantations (Swart et al. 2018). These results agree with those of Yekwayo et al. (2017), which reported that contrasting habitats (natural forest and grassland) showed no overlap of arthropod assemblages, while overlaps were detected between structurally similar habitats (natural forest and pine). As such, similarities in assemblages across sampling points in our study may be linked to the fact that the mining sites were surrounded by grassland (pasture). On the other hand, Swart et al. (2018) showed that beetles are more sensitive to habitat changes than the other taxa with natural forest assemblages not overlapping into the adjacent habitats, while differences in ant assemblages were observed at 20 m into pine and plantation blocks cleared for rehabilitation. Therefore, the argument of shorter distances among our sampling points may not have been the case for all the taxa, given that most of these taxa have limited dispersal abilities.

Effect of distance from the crushed stone mining sites on soil chemical properties

Given that crushed stone mining activities increase the amount of dust produced (Opondo et al. 2022; Pal & Mandal 2017), it is possible that this dust interfered with the soil nutrient composition. The impact of dust on soil chemical properties might have been more severe in close proximity to the mining sites than further away. Thus, we found differences in the composition of soil chemical properties between the sampling point at the edge of the mining sites compared to those further away from the mining activities (50 and 70 m). Although dolerite stone was mined in our sites, Tonello et al. (2021) found that dust from mining agate stone led to changes in soil chemical properties. According to Alloway (2008) weathering of rocks is one of the factors that determine the concentration of zinc in the soil. Therefore, it was not surprising that we recorded greater concentration of zinc at sampling points that are closer to the crushed stone mining sites than those further away. Our results agree with those of a study by Otaraku et al. (2019) in Nigeria, which recorded greater concentration of metals (including zinc) near the rock-crushing area compared to further away. We show that the concentration of zinc in the soil can be used as an indicator of disturbance by crushed stone mining, since the concentrations of other soil chemical properties (calcium, magnesium, phosphorus and pH) did not differ among sampling points. Pal and Mandal (2021) showed that wind can facilitate the spread of stone dust into the surrounding areas, which may increase the size of the areas affected. Therefore, similarities in concentrations of calcium, magnesium, phosphorus and pH among our sampling points may have resulted from crushed stone pollution that affected soils adjacent to the mining sites. Pollution may have been facilitated because the gradients of seven out of the nine transects were steeper with the distance from the mining sites. Our results support previous studies that reported that different soil chemical properties are influenced by crushed stone mining activities differently. For example, in India, Pal and Mandal (2021) recorded alkaline soil pH, low concentration of nitrogen, phosphorous, copper and manganese, while there was higher concentration of zinc near crushed stone activities compared to further away from mining sites. Furthermore, in Nigeria, Adewole and Adesina (2011) found reduced concentration of phosphorus near the mining sites compared to further away from the marble-mining sites.

Surface-active arthropods and soil chemical properties

According to Ashford et al. (2013) the concentration of soil chemical properties (calcium, magnesium, nitrate, carbon, nitrogen and pH) can be influenced by leaf litter depth, with greater concentrations of these properties in plots with deeper leaf litter. Furthermore, abundance of Acari, Araneae, Coleoptera, Diplura and Formicidae increase with an increase in leaf litter depth (Ashford et al. 2013; Silveira et al. 2010). However, in our study, positive correlation was recorded between soil pH and species richness at Blue Rock mining site. In contrast, no other positive correlation was observed between the measured soil properties, and arthropod species richness or abundance. Compared to the study by Ashford et al. (2013), there was no deeper layer of leaf litter in our sites, but the leaf litter was sparsely distributed in our sampling points, and this was not surprising, considering that grass was the dominant vegetation type. Furthermore, Melliger et al. (2018) found a negative correlation between species richness of ants and litter pH. In our study a negative correlation was recorded between arthropod abundance and soil pH at Ikwezi mining site. Although at Blue Rock mining site, a significant moderate positive correlation was recorded between soil pH and species richness, we also observed a non-significant positive correlation between soil pH and arthropod abundance. These results support Zhao et al. (2017) who found a weak positive correlation between arthropod abundance and soil pH.

Sayer et al. (2010) reported that phosphorus, calcium and sodium concentrations are vital in shaping the diversity of arthropods, while the concentrations of sodium and magnesium are vital for arthropod abundance. Even though the soil concentration of calcium in our study did not differ among our sampling points, at Blue Rock mining site, there was a significant strong negative correlation between calcium and arthropod abundance and a non-significant moderate negative correlation between calcium and arthropod species richness. Furthermore, Van der Wal et al. (2009) found a positive correlation between the soil concentration of calcium and the diversity and evenness of plant species, of which herbivorous arthropods increase with plant diversity (Barnes et al. 2020). Therefore, we did not expect a negative correlation between soil concentration of calcium and arthropod species richness and abundance, especially because of the high contents of calcium that Graveland and Van Gijzen (1994) recorded in different arthropod taxa. However, crushed stone mining activities in our study may have increased calcium concentration beyond what arthropods can tolerate. In our study, the zinc concentration in the soil varied across sampling points, with more concentration at 5 m than at 70 m from the mining sites. However, arthropod species richness and abundance did not differ among sampling points. Variations in correlations between soil properties and arthropod species richness and abundance from the two mining sites indicate that other factors (other than crushed stone mining) influence arthropods and soil properties.

Conclusion

Our results found no evidence that crushed stone-mining activities affected assemblages of surface-active arthropods in adjacent vegetation. Crushed stone mining activities did, however, seem to result in an increased concentration of zinc. Although concentrations of other soil chemical properties (calcium, magnesium, phosphorus and pH) did not vary among distances from the mining activities, we found that composition of soil nutrients varied among distances, with greater dissimilarities between the edge (5 m from the mining sites) and sampling points further away from the mining sites.

Acknowledgements

The authors gratefully acknowledge the Blue Rock and Ikwezi mining sites for permission to conduct the study. We are thankful to Mr Sibonelo Mhlongo who assisted with fieldwork, as well as Professor Tarombera Mwabvu for arthropod (millipedes and beetles) identification. We thank the soil analytical laboratory (Department of Agriculture, Land Reform and Rural Development) at Mthatha Dam. In addition, we thank the editors and two anonymous reviewers for their contributions in improving our manuscript.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

I.Y. did the conceptualisation, investigation, methodology, data curation, formal analyses and wrote the original draft. A.M. did the conceptualisation, investigation, methodology, and reviewed and edited the article.

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Supplementary Material

Figure S1. Ikwezi mining site occurring within a matrix of different anthropogenic activities.

Table S1. Abundance and numbers of morphospecies of surface-active arthropods sampled from the two mining sites (Blue Rock and Ikwezi). Abundance and morphospecies of ants are grouped according to subfamilies, while beetles and spiders are grouped according to families, and the other five small taxa according to orders. Morphospecies in beetles and spiders that we could not identify to family are grouped as 'Other'. Subfamilies and/or families of ants, beetles and spiders that had a single morphospecies are listed at the end of that taxon with abundance in parentheses

		Blue Rock		**Ikwezi**	
		Abundance	**Number. of morphospecies**	**Abundance**	**Number of morphospecies**
Ants	Myrmicinae	4 545	27	4 153	21
	Formicinae	979	13	1 292	13
	Dorylinae	30	2	95	1
	Ponerinae	13	3	33	4
		Dolichoderinae (33)		Dolichoderinae (23)	
Beetles	Staphylinidae	82	16	607	23
	Curculionidae	77	15	56	16
	Scarabaeidae	73	12	131	20
	Tenebrionidae	54	4	32	3
	Carabidae	46	10	197	13
	Chrysomelidae	33	11	53	6

		Blue Rock		Ikwezi	
		Abundance	**Number. of morphospecies**	**Abundance**	**Number of morphospecies**
Beetles (continued)	Anthicidae	26	4	29	3
	Scydmaenidae	21	2	42	2
	Buprestidae	7	2	7	2
	Pselaphidae	5	2	22	3
	Nitidulidae			4	3
	Coccinellidae	4	2	4	3
	Elateridae	3	3	728	2
	Histeridae	2	2		
	Other	4	2	22	3
		Erotylidae (8), Nitidulidae (2), Hydrophilidae (1) and Cleridae (1)		Cleridae (3), Hydrophilidae (3), Meloidae (3), Trigidae (3),Cicindelidae (2), Scaphidiidae (1) and Cerambycidae (1)	
Spiders	Lycosidae	452	20	1 570	21
	Gnaphosidae	77	8	105	4
	Salticidae	47	21	33	21
	Zodariidae	53	6	86	8
	Araneidae	34	7	38	9
	Corinnidae	34	7	54	4
	Theridiosomatidae	31	3	39	2
	Nemesiidae	33	2		
	Hahniidae	28	2	13	2
	Theridiidae	9	6	36	4
	Thomisidae	9	3	7	4
	Cyrtaucheniidae	6	2	5	2
	Palpimanidae			6	3
	Clubionidae			6	2
	Pisauridae			3	2
	Scytodidae			3	2
	Other	23	11	36	12
		Miturgidae (4), Oxyopidae (4), Oonopidae (3), Orsolobidae (3), Philodromidae (3), Palpimanidae (2), Idiopidae (2), Ammoxenidae (1), Pholcidae (1), Pisauridae (1) and Selenopidae (1)		Nemesiidae (69), Philodromidae (7), Oxyopidae (6), Oonopidae (4), Orsolobidae (3), Idiopidae (1), Ammoxenidae (1) and Theraphosidae (1)	
Cockroaches	Blattodea	26	12	29	8
Millipedes	Odontopygida	41	8	42	12
	Spirostreptida	8	3	11	4

		Blue Rock		Ikwezi	
		Abundance	**Number. of morphospecies**	**Abundance**	**Number of morphospecies**
Millipedes (continued)	Sphaerotheriida			3	2
		Polydesmida (118), Sphaerotheriida (1)		Polydesmida (19)	
Centipedes	Lithobiomorpha	10	2	24	5
		Geophilomorpha (2)		Geophilomorpha (2)	
Scorpions	Scorpiones	3	2		
Pseudoscorpions		Pseudoscorpiones (2)			

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BOTHALIA – African Biodiversity & Conservation
ISSN: (Online) 2311-9284, (Print) 0006-8241

Role of *Vachellia karroo* as a nurse plant in old fields targeted for passive restoration

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Dates
Submitted: 1 December 2023
Accepted: 17 April 2024
Published: 8 August 2024

How to cite this article:
Mlonzi, V. & Ruwanza, S., 2024, 'Role of *Vachellia karroo* as a nurse plant in old fields targeted for passive restoration', *Bothalia* 54, a8. http://dx.doi.org/10.38201/btha.abc.v54.8

Background: In degraded environments such as old fields, nurse plants can facilitate the growth of targeted restoration plant species by ameliorating extreme environmental conditions, creating nutrient-rich microclimates and protecting recruiting plants from grazing.

Aim & objectives: This study examined the role of *Vachellia karroo* (Hayne) Banfi & Galasso as a nurse plant on soil physical and chemical properties and vegetation diversity in old fields targeted for passive restoration at the Tanglewood research farm in the Eastern Cape, South Africa.

Methods: Soils were quantified for physical and chemical properties in 48 plots measuring 25 m^2 (5 × 5 m) that were located under and outside 24 *V. karroo* nurse plants in old fields. In addition, detailed vegetation surveys were conducted in the above-mentioned plots.

Results: Our results show that soil total nitrogen (N) and carbon (C) concentrations were higher under than outside *V. karroo* nurse plants. Soil penetration resistance and water-repellency levels were lower under than outside *V. karroo* nurse plants, however, monthly variations were also observed. Species richness and Shannon-Wiener diversity were higher under than outside *V. karroo* nurse plants, with species such as *Searsia crenata, Azima tetracantha, Asparagus africanus* and *Opuntia* sp. frequently occurring under *V. karroo* nurse plants.

Conclusion: The study concludes that *V. karroo* nurse plants have a positive effect on some soil physical and chemical properties and vegetation diversity. It is recommended that *V. karroo* needs to be included in future old field restoration strategies if passive restoration at Tanglewood research farm is to be successful.

Keywords: nurse plant syndrome, ecological restoration, plant-to-plant facilitation, pioneer plants, soil nutrients.

Introduction

The establishment of native woody plants in abandoned agricultural fields (hereafter old fields) targeted for passive restoration is constrained by several factors that include soil legacy effects linked to past cultivation, lack of native plant soil seedbanks, grazing, fire and harsh environmental conditions that suppress plant establishment (Badano et al. 2016; Uselman et al. 2018). Nevertheless, some woody plants can overcome the above-mentioned constraints and establish in old fields as nurse plants that kickstart the restoration process through positive plant-to-plant facilitation (Navarro-Cano et al. 2019). Nurse plants are defined as plant species that positively facilitate the growth and establishment of other plant species beneath their canopy (Ren et al. 2008). Several studies have shown that nurse plants create microhabitats underneath them that are favourable for germination and growth of other plant species (Ren et al. 2008; Navarro-Cano et al. 2019; Ruwanza 2019). They also protect plants underneath from herbivore damage, mostly preventing grazing and trampling (Ren et al. 2008). For example, Navarro-Cano et al. (2019) showed that the nurse plant species *Pinus halepensis*, *Osyris lanceolata* and *Atriplex halimus*, promote positive plant–microbial interactions that benefit other recruiting plants, thus facilitating their growth. Ruwanza (2019) reported that soils underneath the nurse plants *Vachellia nilotica*, *Peltophorum africanum* and *Senegalia nigrescens* had improved soil properties such as moisture and soil penetration resistance compared to soils outside nurse plants. The above-mentioned examples show that nurse plants play an important role in facilitating the establishment of other plants (Ren et al. 2008; Navarro-Cano et al. 2019).

Few studies have examined the role of nurse plants in old fields targeted for passive restoration (Padilla et al. 2004; Padilla & Pugnaire 2006; Ruwanza 2019), especially in South Africa were old fields are on the increase due to several economic (declining farming profits), social (urban migration) and environmental (climate change) factors (Blair et al. 2018). Elsewhere, studies on the role of nurse plants in old fields have shown that nurse plants such as *Retama sphaerocarpa* enhance the germination and seedling survival of other plants like *Olea europaea* in semi-arid old fields of Almeria, Spain (Padilla et al. 2004). In another study, Padilla and Pugnaire (2006) concluded that targeted restoration species tend to survive and grow better underneath nurse plants in old fields, thus the need to include nurse plants in old field restoration guidelines. In South Africa, Ruwanza (2019) showed that the diversity of native plants was higher underneath nurse plants in 35-year-old Lapalala Wilderness old fields, an indication that nurse plants need to be protected from grazing so that they act as restoration foci.

The above-mentioned studies seem to suggest that several mechanisms explain the positive role of nurse plants in old field restoration (Ren et al. 2008; Navarro-Cano et al. 2019; Ruwanza 2019). These mechanisms include improved microclimatic conditions underneath nurse plants, increased soil moisture and nutrient availability underneath nurse plants, and protection of native plants against environmental and external stresses like heat and herbivory (Padilla & Pugnaire 2006; Ruwanza 2019). Ren et al. (2008) and Lopez et al. (2007) used the term nurse plant syndrome to explain the positive effects of nurse plants on native species underneath. Within old fields, such positive effects of 'nurse plant syndrome' could include abiotic stress amelioration, e.g., shade provided by nurse plants can improve soil moisture content underneath the plant, resulting in enhanced seedling establishment and growth. A recent study by Ruwanza (2022) showed that the presence of nurse plants in old field ridges creates nutrient-rich islands underneath the plants, which could facilitate plant growth underneath.

Although there is consensus among restoration ecologists that nurse plants could potentially play a key role in facilitating passive old field restoration (Padilla & Pugnaire 2006), few studies have been conducted in South Africa (Ruwanza 2019), where land abandonment is on the increase (Blair et al. 2018). Besides, for South Africa to meet its ecological restoration targets aimed at achieving land degradation neutrality by 2030 (Von Maltitz et al. 2019), more research is needed to unpack the restoration dynamics in old fields, particularly the role of nurse plants in facilitating passive restoration. Apart from that, old field restoration trajectories might differ due to several factors like soil legacy effects and cultivation history, therefore there is a need to assess passive restoration dynamics in old fields across different environments to develop adaptive interventions.

Assessing the positive effects of nurse plants on underneath recruiting plant species requires determining if facilitation is occurring (Navarro-Cano et al. 2019). It is generally assumed that facilitation occurs when ecological benefits underneath the species are displaying positive co-occurrence patterns that are evident at multiple locations (Badano et al. 2016; Uselman et al. 2018). However, it is important to note that nurse plant facilitation could take time depending on several factors like degradation extent, rate of nurse plant establishment, and other external factors like fire, grazing and climate change (Ren et al. 2008). Nonetheless, nurse plant facilitation is not only measured from a plant co-occurrence standpoint, but some studies have looked at it from a species diversity and community dynamics standpoint (Navarro-Cano et al. 2015). Examples are in dry arid regions where nurse plants provide refuge for diverse species that could probably fail to establish outside nurse plants due to harsh environmental conditions (Pérez-Sánchez et al. 2015). However, the role of nurse plant facilitation needs to be examined from both a soil and vegetation standpoint, particularly understanding plant and soil changes since they are essential in understanding ecosystem functioning. Indeed, plant-soil interactions and feedback can significantly influence species recruitment in old fields, thus ultimately playing a key role in regulating vegetation recovery trajectory (Ruwanza 2019).

Few studies have looked at how nurse plants promote changes in soil physical and chemical properties and how this can regulate plant diversity and community structure underneath nurse plants (Navarro-Cano et al. 2015; Ruwanza 2019). Navarro-Cano et al. (2015) showed that nurse plant canopy cover can facilitate changes in litter quantity, which ultimately alters soil nutrients. However, changes in soil physical and chemical properties due to nurse plants could be determined by several factors, such as nurse plant type, age and litter release, as well as other external factors, such as microbial activity underneath the nurse plant (Navarro-Cano et al. 2015, 2019). Indeed, studies on the effects of nurse plants on soil physical and chemical properties are long overdue if the facilitative role of nurse plants in old fields is to be fully understood. Given the high costs of assisted old field restoration (active restoration), research on the role of nurse plants in old fields can provide valuable information to enrich our understanding of the natural succession patterns in old fields. Theoretically, nurse plants can enhance germination and growth of underneath recruiting native plants in old fields; however, positive and negative feedback interactions can occur, thus shifting recruitment dynamics and plant composition structure (Callaway et al. 2002). For example, positive plant-soil interactions can facilitate increased plant diversity underneath nurse plants, yet negative interaction can trigger dominance of one species thus triggering bush encroachment or alien plant invasion. This needs to be tested to assess the facilitative role of nurse plants in germination and growth of native plants that can trigger passive restoration in old fields.

In this study, we assessed the influence of the *V. karroo* nurse plant on soil physical and chemical properties and underneath vegetation diversity in old fields targeted for passive restoration at Tanglewood research farm in the Eastern Cape, South Africa. Based on the nurse plant facilitation theory, the research questions were: (i) does the nurse plant *V. karroo* facilitate changes in soil physical and chemical properties underneath its canopy; and (ii) does the nurse plant *V. karroo* affect vegetation diversity underneath its canopy? We predict that old fields are resource-limited environments, and the *V. karroo* nurse plant will create positive plant–soil feedback that creates suitable conditions for soil and vegetation recovery underneath its canopy compared to areas outside its canopy. Our prediction is centred on existing knowledge related to nurse plant syndrome and associated amelioration effects (Lopez et al. 2007).

Materials and methods

Study area

The study was conducted in old fields located at Tanglewood research farm (33°30′57.57″S, 26°14′59.70″E), which is approximately 45 km from the town Makhanda (previously Grahamstown) in the Eastern Cape, South Africa (Figure 1). The 760-hectare ex-privately owned dairy farm is currently used as a conservation farm with a few wild animals, such as Cape mountain zebra (*Equus zebra zebra*) and giraffe (*Giraffa camelopardalis*). Due to the change of property ownership, it is not clear when crop cultivation and subsequent dairy farming were abandoned; however, personal communication with the current manager (Dylan Blew in 2024) and Google Earth images seem to suggest that cultivation was last done in

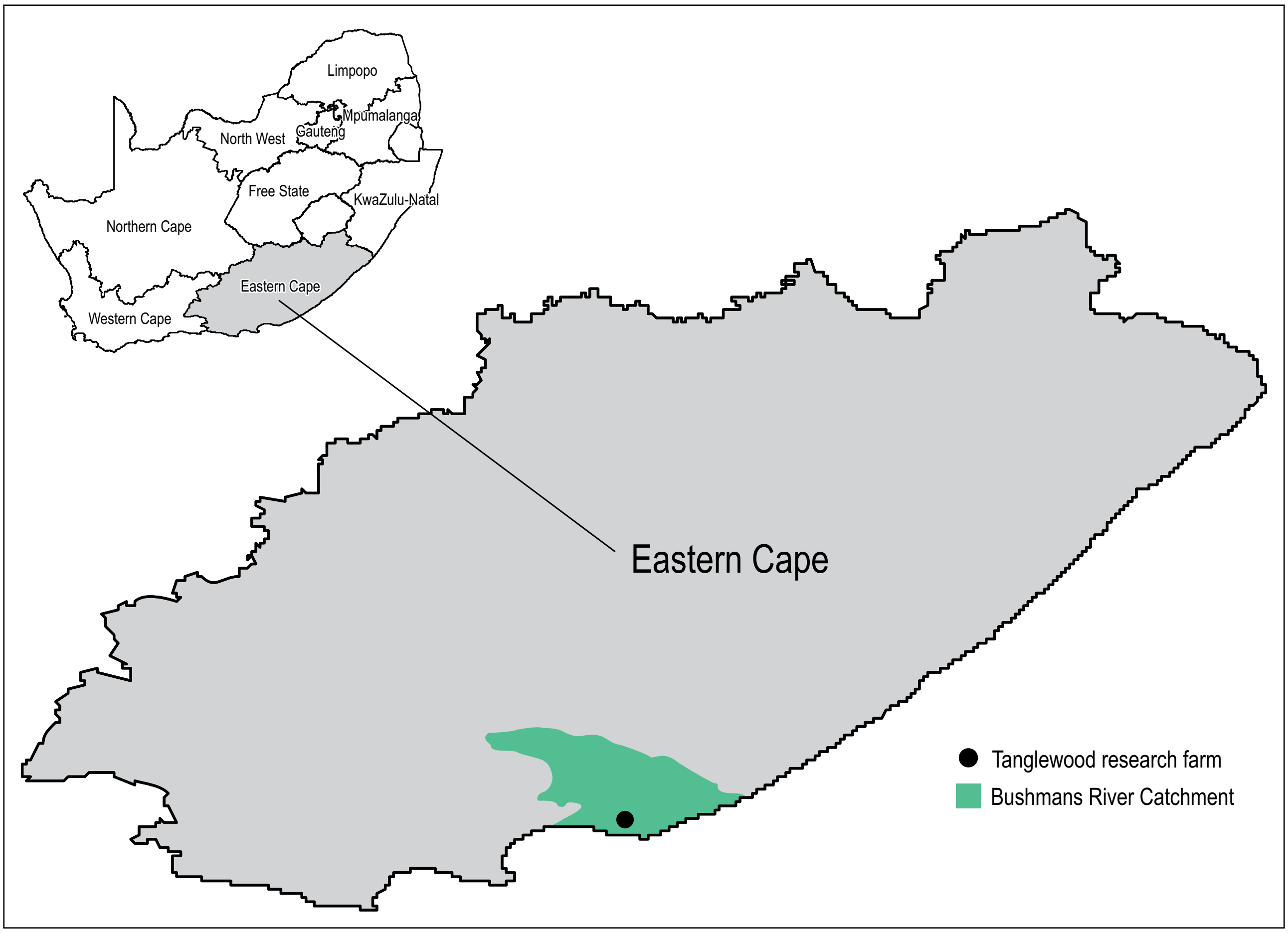


Figure 1. Map showing the location of the study area in the Eastern Cape, South Africa.

2008. Tanglewood research farm is earmarked for upscaling Albany Thicket restoration. As a result, a restoration trial to introduce a mixture of Albany Thicket species, including the ecosystem engineer *Portulacaria afra* (Van der Vyver et al. 2013), is being implemented in the old fields. The vegetation type in the study area falls within the Albany Thicket biome and is known as Kowie Thicket (Hoare et al. 2006). Although the geology in this region is complex, soils in the study area is predominantly clay and sand of the Weltevrede and Darlington formations. Vegetation is dominated by succulent euphorbias, aloes and understorey shrubs such as *Capparis*, *Secamone* and *Rhoicissus* species (Hoare et al. 2006). Although rainfall is nonseasonal, most rain falls in austral summer, with optima in March and October/November (Hoare et al. 2006). The mean annual precipitation is 650 mm and temperatures range from an average of 35°C in summer to 6°C in winter (Hoare et al. 2006).

Nurse plant

Vachellia karroo (formerly *Acacia karroo* and commonly known as sweet thorn), is the dominant tree in the old fields study site. It is indigenous to southern Africa and belongs to the Fabaceae family (Beukes et al. 2019). The tree is widely distributed in southern Africa and grows in different soil types, biomes, climatic and edaphic conditions (Taylor & Barker 2012; Dingaan & Du Preez 2018; Beukes et al. 2019). The tree can resist salinity, fire, drought and frost, which contribute towards its dominance and expansion in degraded ecosystems such as old fields, thus being regarded as an expansive bush encroacher, or pioneer species (Dingaan & Du Preez 2018). Like most legumes, *V. karroo* fixes nitrogen into the soil by forming mutualistic symbioses with *Rhizobium* soil bacteria (Beukes et al. 2019). *Rhizobium* bacteria converts atmospheric nitrogen to nitrogen compounds that can be used to enhance *V. karoo* growth (Dingaan & Du Preez 2018). Apart from that, *V. karroo* can uptake water and nutrients from deep underground soils, which can be used to increase its growth (Dingaan & Du Preez 2018).

The plant grows to a height of 5 to 12 m in disturbed areas and to more than 20 m in undisturbed areas like riparian zones where growth conditions are favourable (Dingaan & Du Preez 2018). *Vachellia karroo* is usually single stemmed, branching low on the trunk and has a rounded crown (Dingaan & Du Preez 2018). Leaves are generally dense and dark green in colour. Flowers are yellow and the pods are flat and sickle-shaped (Dingaan & Du Preez 2018). The tree has many uses that include: (i) medicinal properties in the leaves and bark for diarrhoea treatment; (ii) pods and fruits for livestock fodder; (iii) flowers for honey production; and (iv) seeds that can be roasted and used as a coffee substitute (Van Wyk 2011; Cock & Van Vuuren 2015; Dingaan & Du Preez 2018). Its nurse plant properties have resulted in the plant being used as an indicator for surface and groundwater availability, as well as for good grazing sweetveld (Dingaan & Du Preez 2018; Beukes et al. 2019).

Experimental design

Three old fields of varied sizes ranging from 125 000 m^2 to 969 000 m^2 were purposively selected in April 2022. Purposive sampling was done to allow old fields dominated by *V. karroo* to be selected. The selected old fields were approximately 1 km apart and dominated by *V. karoo* and low grass cover, mainly *Cynodon dactylon, Aristida junciformis* and *Paspalum distichum* in open patches. In each of the above-mentioned old fields, eight *V. karroo* nurse plants were purposively selected for soil and vegetation measurements. The eight selected plants per old field were approximately 50 m apart to minimize sampling plants that are close to each other. Nurse plants were purposively selected based on the following minimum requirements: (i) height of 4.5 m; (ii) diameter at breast height of 70 cm; and (iii) tree crown of 7.5 m. Tree height was measured using a sectional measuring pole, whereas diameter at breast was measured using a digital vernier calliper. Tree crown, a measure of canopy area of influence on the ground was measured using a tape measure. We acknowledge that purposive selection of nurse plants is prone to sampling bias that could have implications on generalisation of results, however it was used to give us insights on the role of nurse plants on soil and vegetation recovery. Using the selected tree as the centre of the plot, a 25 m^2 (5 × 5 m) plot was set up underneath the canopy of each selected nurse plant tree (the plots were referred to as under nurse plants with 100% *V. karoo* canopy cover). To assess if changes in both soil and vegetation underneath the nurse plants were a result of the selected plants, plots with similar above-mentioned dimensions were set up 5 m away from the nurse plant plot boundary (the plots were referred to as outside nurse plants – with less than 75% grass and forb cover). For consistency, all outside nurse plant plots were placed on the east side of the under-nurse plant plot. In total, 48 plots were surveyed [8 replicated trees ×2 locations (under and outside) ×3 old fields].

Soil measurements

Topsoil cores measuring 10 cm in diameter and 10 cm in depth were collected as close to the centre of all the plots, after the removal of overlying debris. After soil collection, soils were transported immediately to Rhodes University laboratory for gravimetric soil moisture and soil water repellency measurements, which were conducted over a three-month period from May to July 2022. A subset of the collected soil samples were sent to a commercial laboratory, namely Bemlab (Pty) Limited, for macro element (N, C and P), pH and exchangeable cation (K, Ca, Mg, Na) measurements.

Soil penetration resistance levels and soil water infiltration measurements were conducted in all plots over the above-mentioned three-month period.

Prior to laboratory measurements, soils were sieved using a 2 mm sieve to remove stones and plant debris. Gravimetric soil moisture content was measured by weighing soil samples wet, oven drying them for 72 hours at 105°C, and re-weighing them to obtain moisture content, which was then converted to a percentage (Black 1965). Soil water repellency was measured using the Water Droplet Penetration Time (WDPT) method as described by Bisdom et al. (1993) and Doerr and Thomas (2000). Sieved soils were placed in Petri dishes and air-dried for seven days under laboratory conditions. After drying, the WDPT test was conducted by placing four drops of distilled water onto the soil surface and recording the time taken by each drop to penetrate the soil. The drops were placed using a syringe, and the average time (in seconds) for the four drops was taken to represent the WDPT per sample. The WDPT classes used in the study were adopted from Bisdom et al. (1993) as wettable (below 5 s), slightly water repellent (5–60 s), strongly water repellent (60–600 s), severely water repellent (600–3 600 s) and extremely water repellent (above 3 600 s).

Soil pH was analysed in 1:5 soil-KCl extract as described by Rhoades (1982). Soil phosphorus (P) was analysed using a Bray-II extract method as described by Bray and Krutz (1945). Soil total nitrogen (N) was determined by complete combustion using a Eurovector Euro EA Elemental Analyser, whilst soil total carbon was determined using a modified Walkley-Black method as described by Chan et al. (2001). Exchangeable cations, namely potassium (K^+), calcium (Ca^+), magnesium (Mg^+), sodium (Na^+), were extracted in a 1:10 ammonium acetate solution using the centrifuge procedure (Thomas 1982). The samples were then filtered, and analysed by atomic absorption spectrometry (SP428, LECO Corporation, USA). Soil penetration resistance levels were measured using a pocket penetrometer (SOILTEST, Inc.), as described by Leung and Meyer (2003). Soil infiltration was measured using a mini disc infiltrometer (Decagon Devices 2014). The infiltrometer was filled with water in both the upper and lower chambers and placed on the soil surface after hand removal of litter and debris. After every 30 seconds for 5 minutes, the level of water infiltrating into the soil was measured from the drop of water level in the lower chamber of the infiltrometer in ml. The level of infiltration rate was determined from the measured cumulative infiltration rates over time as described by Zhang (1997).

Vegetation measurements

Within each plot, a detailed vegetation survey was conducted in June 2022. Grasses and annual forbs were excluded during vegetation surveys since they were dry and tended to die back in winter. The richness and abundance of perennial trees, shrubs and forbs were determined through counting the total number of individual plant species present in the entire plot. Plant samples were collected and visually identified in conjunction with local plant books (Manning 2007, Manning & Goldblatt 2012) and the PlantzAfrica online directory (South African National Biodiversity Institute 2017). Those that could not be positively identified were sent to Selmar Schonland Herbarium in Makhanda.

Data analysis

Prior to selecting an appropriate statistical test to test for differences between under and outside nurse plants, all quantitative datasets were tested for normality using the Kolmogorov-Smirnov test and homogeneity of variance using Levene's test, and data was normally distributed. Comparisons between under and outside nurse plants for measured soil properties of N, C, P, pH, K, Ca, Mg and Na were done using a t-test since the data was collected once. Gravimetric soil moisture, soil penetration resistance levels, and infiltration rates were analysed using repeated measures ANOVA since data was collected monthly over a three-month period. Comparisons between under and outside nurse plants for WDPT were done using Chi-squared goodness of fit test since the WDPT data were categorical. Species abundance, richness, Shannon-Wiener diversity, Simpson's index of diversity, and Evenness index were calculated per plot and analysed between under and outside nurse plants using a t-test since data was collected once. All statistical analyses were done using TIBCO STATISTICA version 13.0 software (TIBCO Software Inc 2019).

Results

Effect of nurse plant *Vachellia karroo* on soil properties

Soil from under and outside the sampled nurse plants were made up of sand (87%) and loam (13%) soils. Soil in the study area were strongly acidic and pH was significantly ($p < 0.05$) higher outside than under nurse plants (Table 1). In contrast, soil P showed no significant ($p > 0.05$) differences between under and outside nurse plants (Table 1). Measured soil total C and N were significantly ($p < 0.01$) higher under than outside nurse plants (Table 1). Soil N was twice as high under as compared to outside nurse plants. Of the measured micronutrients, only Ca and Mg were significantly ($p < 0.05$) higher under than outside nurse plants (Table 1). Soil K and Na did not show any significant ($p > 0.05$) differences between under and outside nurse plants (Table 1).

Table 1. Comparison of measured soil chemical properties under and outside nurse plants. Data are means ± SE and t-test results are shown

Soil property	Under nurse plants (n = 24)	Outside nurse plants (n = 24)	t-value	p-value
pH	5.48 ± 0.14	5.95 ± 0.16	2.15	0.041
P Bray II (mg/kg)	37.73 ± 5.70	42.15 ± 7.81	0.46	0.651
N (%)	0.18 ± 0.02	0.09 ± 0.01	3.62	0.001
C (%)	1.35 ± 0.14	0.84 ± 0.04	3.39	0.002
K (mg/kg)	232.27 ± 20.07	288.74 ± 29.05	1.60	0.121
Ca (mg/kg)	5.10 ± 0.74	3.11 ± 0.37	2.40	0.023
Mg (mg/kg)	1.56 ± 0.18	1.12 ± 0.12	2.06	0.049
Na (mg/kg)	0.22 ± 0.02	0.35 ± 0.09	1.40	0.172

Comparisons between under and outside nurse plants showed no significant ($p > 0.05$) differences in gravimetric soil moisture content for all three months (Figure 2A). However, monthly comparisons in gravimetric soil moisture content varied, with significantly ($p < 0.001$) higher soil moisture content being reported in May and July as compared to June (Figure 2A). Interactions between nurse plant location and months for soil moisture content showed no significant ($p > 0.05$) differences (Figure 2A). Soil penetration resistance was significantly ($p < 0.001$) higher outside than under the nurse plants for all three months (Figure 2B). However, the above-mentioned differences were more visible in May, where soil penetration resistance levels were twice as high outside than under nurse plants. Monthly comparisons on soil penetration resistance showed significant ($p < 0.01$) differences for all three months, with higher soil penetration resistance levels being recorded

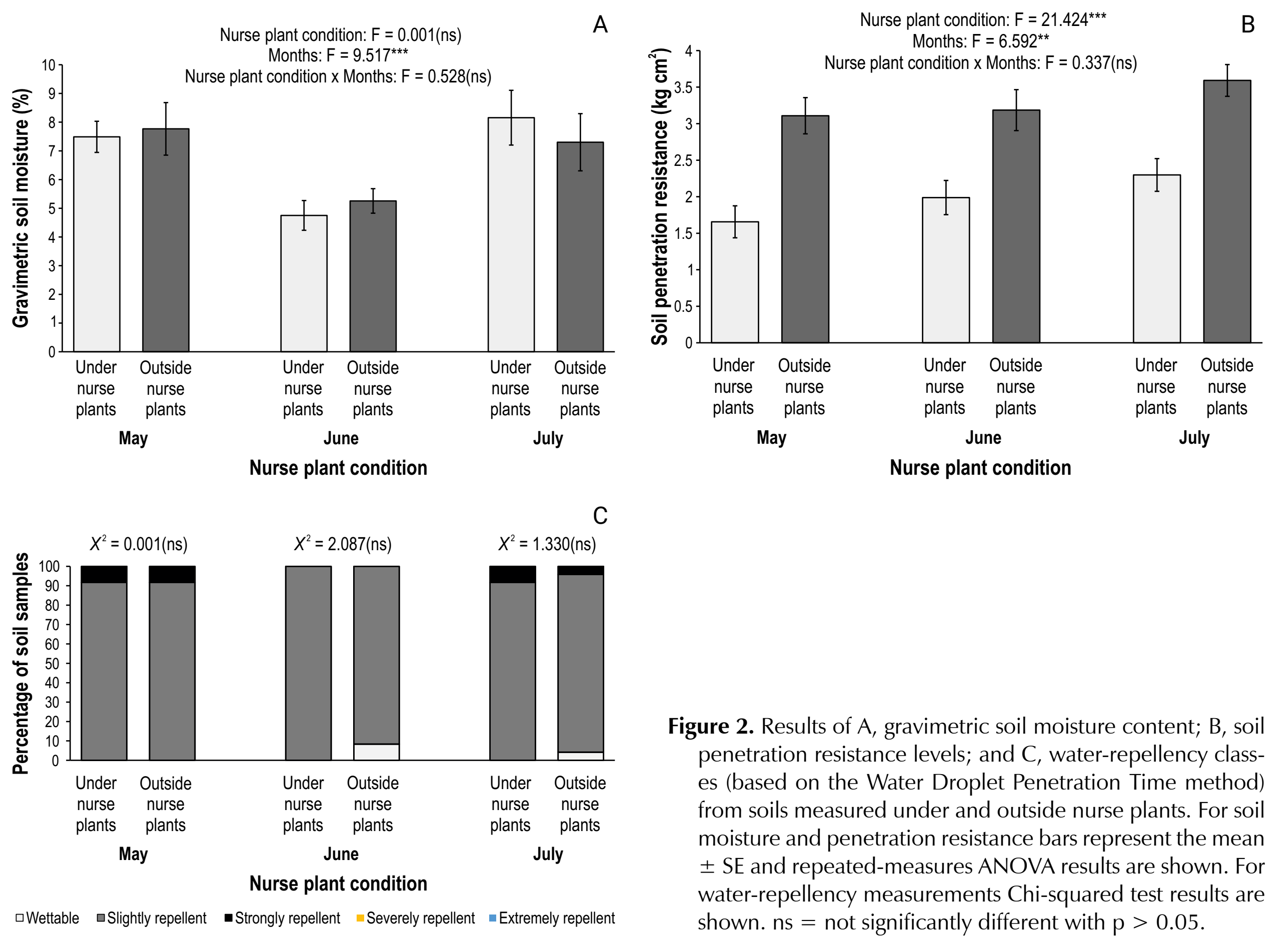


Figure 2. Results of A, gravimetric soil moisture content; B, soil penetration resistance levels; and C, water-repellency classes (based on the Water Droplet Penetration Time method) from soils measured under and outside nurse plants. For soil moisture and penetration resistance bars represent the mean ± SE and repeated-measures ANOVA results are shown. For water-repellency measurements Chi-squared test results are shown. ns = not significantly different with $p > 0.05$.

in June and July than in May (Figure 2B). Interactions between nurse plant location and months for soil penetration resistance showed no significant (p > 0.05) differences (Figure 2B).

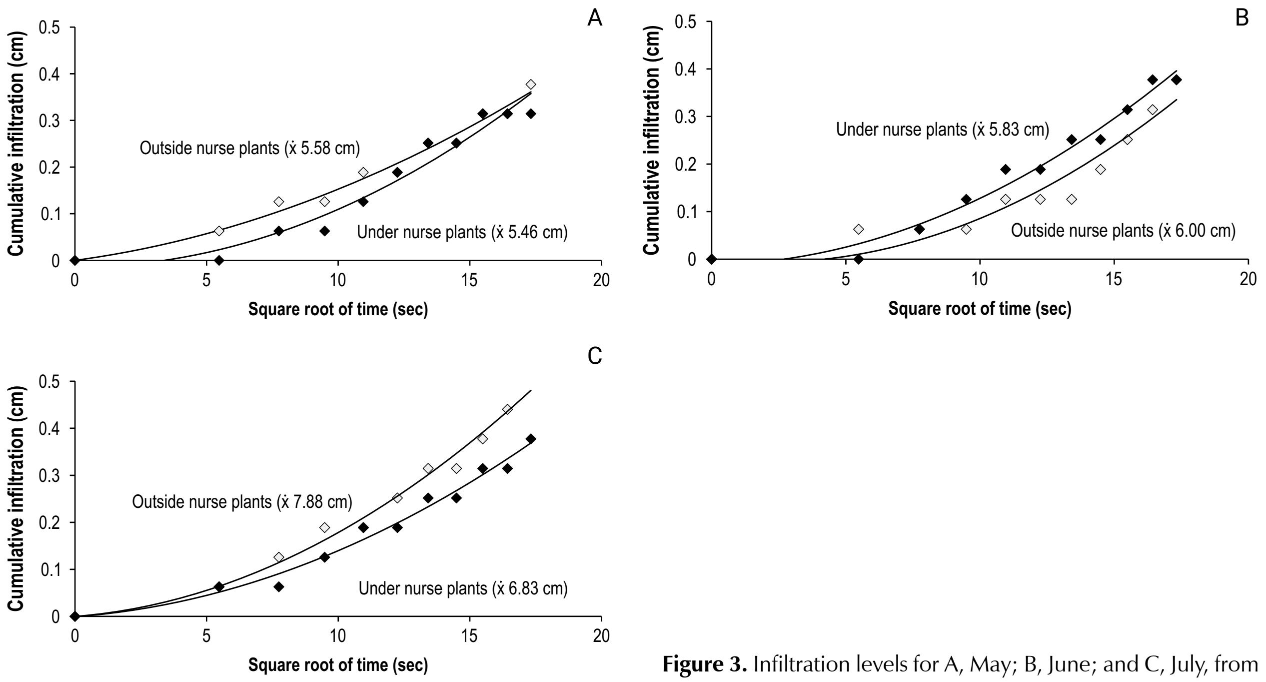
Most soils collected under and outside nurse plants were slightly repellent (more than 92%) for all the three months (Figure 2C). During the month of May, only 8% of the soils were strongly repellent under and outside nurse plants. In July, 8% of the strongly repellent soils were recorded under nurse plants as compared to 4% recorded outside nurse plants. Wettable soils were recorded outside nurse plants in the month of June (8%) and July (4%) only (Figure 2C). The chi-squared test on soil water repellency categories indicated no significant (p > 0.05) differences between under and outside nurse plants for all months (Figure 2C).

Infiltration rates showed no significant (p > 0.05) differences between under and outside nurse plants for all months (Figure 3). The average infiltration rate was 5.46 ± 0.83 cm under nurse plants in May as compared to 5.58 ± 0.79 cm outside nurse plants. In June, the difference in infiltration rates after 5 minutes between under (mean = 5.83 ± 1.85 cm) and outside (mean = 6.00 ± 0.90 cm) nurse plants was 0.17 cm. During July, the average infiltration rate after 5 minutes was 6.38 ± 1.28 cm under nurse plants as compared to 7.89 ± 1.57 cm outside nurse plants (Figure 3C). Although the month of July had the highest average soil infiltration rate (mean = 7.14 cm after 5 minutes) as compared to June (mean = 5.92 cm after 5 minutes) and May (mean = 5.52 cm after 5 minutes), statistical monthly comparisons showed no significant (p > 0.05) differences for all three months. Similarly, interactions between nurse plant location and months for soil infiltration rate showed no significant (p > 0.05) differences (Figure 3).

Effect of nurse plant *Vachellia karroo* on vegetation

Although species abundance was higher under as compared to outside nurse plants, statistical comparisons showed no significant (p > 0.05) differences between the two locations (Table 2). In contrast, species richness was significantly (p < 0.001) higher under than outside nurse plants (Table 2). Shannon-Wiener showed significant (p < 0.001) differences between under and outside nurse plants, being higher under than outside nurse plants (Table 2). Simpson's diversity and species evenness showed no significant (p > 0.05) differences between under and outside nurse plants.

Seven plant species, namely *V. karroo, Searsia crenata, Azima tetracantha, Amaranthus* sp., *Asparagus africanus, Bulbine* sp. and *Opuntia sp.*, had frequency occupancy of more than 50% under nurse plants as compared to only three species, namely *Amaranthus* sp., *Selago* sp. and *Drosanthemum hispidum*, outside nurse plants (Table 3). Four of the above-mentioned



Nurse plant condition: F = 0.35 (ns)
Months: F = 0.85 (ns)
Nurse plant condition x months: F = 0.19 (ns)

Figure 3. Infiltration levels for A, May; B, June; and C, July, from soils measured under and outside nurse plants. The results of the repeated-measures ANOVA (based on the average infiltration rate after 5 min) are shown; ns = not significantly different with p > 0.05.

Table 2. Comparison of measured vegetation diversity indices under and outside nurse plants. Data are means ± SE and t-test results are shown

Vegetation indices	Under nurse plants	Outside nurse plants	t-value	p-value
Species abundance	52.75 ± 5.60	45.96 ± 4.35	0.96	0.343
Species richness	5.75 ± 0.37	3.96 ± 0.34	3.56	0.001
Shannon-Wiener	1.38 ± 0.05	1.08 ± 0.05	3.99	0.001
Simpson's diversity	0.72 ± 0.02	0.66 ± 0.05	1.21	0.234
Species evenness	0.81 ± 0.02	0.84 ± 0.02	1.09	0.281

frequently occurring species, namely *V. karroo, S. crenata, Azima tetracantha* and *Asparagus africanus,* were present under nurse plants but not outside nurse plants. Only *Ammocharis coranica* was not present under nurse plants (Table 3).

Discussion

Our results support our prediction that *V. karoo* nurse plant creates positive plant-soil feedback that creates suitable conditions for soil and vegetation recovery underneath its canopy. We observed improved soil C, N, Ca, Mg, penetration resistance and vegetation diversity (species richness and Shannon-Wiener index) underneath *V. karroo* nurse plants compared to outside. However, some soil properties showed no differences between underneath nurse plants and outside, an indication that results could be varied. The abovementioned soil results seem to suggest that the nurse plant *V. karroo* plays a significant role in improving some soil physical and chemical properties. Previous studies have reported similar results where the effects of nurse plants on soil properties were varied (Mihoč et al. 2016; Navarro-Cano et al. 2018, 2019; Ruwanza 2019). Mihoč et al. (2016) assessed ten nurse plants in the central Chilean Andes and concluded that soil under nurse plants were rich in nutrients as compared to barren soils outside, although this varied with plant type, altitude and soil type. Navarro-Cano et al. (2018) reported that nurse plants increase soil fertility and microbial productivity in degraded ecosystems such as

Table 3. List of 28 frequently occurring plant species present under and outside nurse plants. '*' species was present and is based on calculated species occupancy frequencies categorised as: * (1–25%), ** (26–50%), *** (51–75%) and **** (76–100%); '-' species not present

Species name	Under trees	Outside trees
Achyropsis leptostachya	**	*
Aizoon glinoides	*	*
Aloe sp.	*	-
Amaranthus sp.	***	***
Ammocharis coranica	-	**
Asparagus africanus	***	-
Asparagus asparagoides	*	*
Asparagus striatus	*	*
Azima tetracantha	***	-
Bulbine sp.	***	**
Crassula expansa	*	*
Delosperma sp.	*	*
Drosanthemum hispidum	**	***
Exomis sp.	*	*
Hermannia althaeoides	*	*
Isoglossa sp.	*	-
Kalanchoe sp.	**	-
Lycium ferocissimum	**	*
Lycium oxycarpum	**	*
Olea europaea subsp. *cuspidata*	*	*
Opuntia sp.	***	*
Searsia crenata	***	-
Selago sp.	*	***
Senecio deltoideus	*	-
Solanum sisymbriifolium	*	-
Teucrium africanum	*	**
Teucrium sp.	*	-
Vachellia karroo	****	-

abandoned mine dumps. Ruwanza (2019) showed that the dominance of three nurse plants, namely *V. nilotica*, *Peltophorum africanum* and *Senegalia nigrescens* in Lapalala Wilderness old fields resulted in positive soil recovery trajectory, with soils under nurse plants canopy showing improved soil moisture and penetration resistance than soils outside. Several factors, such as increased plant litter, role of nurse plant canopy, improved microbial activities, and positive plant-soil feedback have been used to explain why soil underneath nurse plants have improved soil properties (Ren et al. 2008; Mihoč, et al. 2016; Navarro-Cano et al. 2019).

Although not measured in this study, increased litter deposition has been shown to be linked to increased litter biomass, creation of soil fertile microsites beneath nurse plants, and increased microbial productivity (Navarro-Cano et al. 2019). Stuart-Hill et al. (1987) reported that *V. karroo* deposits high litter quantities in soils, which influences soil nutrients and subsequently explains the observed high nutrients underneath *V. karroo* trees. Increased plant litter underneath nurse plants can impact both soil organic matter, bacterial and fungal diversity (Pérez-Valera et al. 2018). Both increased soil organic matter and bacterial diversity affect soil microbial processes such as decomposition and nutrient cycling (Zak et al. 2003), this is likely to explain why soil C and N concentrations were high underneath *V. karroo* nurse plants. Besides the above, *V. karroo* is a known nitrogen-fixing leguminous tree (Dingaan & Du Preez 2018), this is likely to explain the high soil N levels underneath the plant. Leguminous trees form symbiotic relationships with rhizobia (nitrogen-fixing bacteria), which converts nitrogen into ammonia that can be used by the plant. Several studies on leguminous trees such as *V. karroo* and acacias (although invasive alien plants in South Africa) have reported high soil N concentrations underneath these plants and attributed this to the nitrogen-fixing process (Dingaan & Du Preez 2018). Although the actual nitrogen-fixation quantities in soils remain unknown, Dingaan and Du Preez (2018) reported that *V. karroo* fixes nitrogen in the soils, thus enhancing soil fertility underneath it through the creation of nutrient-rich islands. Although our study did not observe soil moisture differences under and outside nurse plants, moist soils underneath nurse plants are known to enhance bacterial and mycorrhizal activity, which have a positive effect on soil nutrient availability (Manzoni et al. 2014; Sierra et al. 2017).

Nurse plants have been shown to create fertile soil islands underneath their canopy (Callaway et al. 2007; Mihoč et al. 2016). These zones of nutrient enrichment underneath nurse plants are a result of a wide range of interacting biotic and abiotic mechanisms (Stock et al. 1999). For example, nitrogen fixation, hydraulic uplift, plant nutrient uptake from surrounding soils, and trapping of windblown and animal transported organic material by plants could explain why some high soil nutrient concentrations were observed underneath nurse plants (Stock et al. 1999). In this study, hydraulic uplift (the process of water movement from wet to dry soil layers through roots) by *V. karroo* roots could explain why some soil properties were high under nurse plants. *Vachellia karroo* has deep long taproots (up to 50 m) that can allow it to extract water from deep underground through hydraulic uplift (Dingaan & Du Preez 2018). This process can benefit soil around the nurse plant in several ways. Firstly, *V. karroo* can increase its daily water uptake because of hydraulic uplift, thus increasing its growth and subsequent litter deposition, which has been shown to benefit soil nutrients (Emerman & Dawson 1996). Secondly, hydraulic uplift can positively affect surrounding plant communities, particularly understorey vegetation, through increased uptake of soil moisture and nutrients being made available through *V. karroo* hydraulic uplift (Ludwig et al. 2003). Improved plant abundance and diversity underneath nurse plants can, in turn, improve soil properties indirectly through increased litter deposition, thus facilitating positive plant–soil feedback. Lastly, hydraulic uplift can increase mineralisation rates, thus maintaining bacterial activities during dry periods, which has a positive effect on soil nutrient concentrations (Ludwig et al. 2003).

Our results showed that nurse plants have a positive effect on vegetation diversity, given that we recorded more plants underneath *V. karroo* nurse plants as compared to outside. This observation concurs with results from other studies where the diversity and abundance of other plants were high under nurse plants as compared to outside (Badano et al. 2016; Ruwanza 2019). Badano et al. (2016) reported that most plant species were positively associated with the nurse plant *Larrea tridentata*. The same above-mentioned study also identified high seed density under *L. tridentata,* an indication that the nurse plant traps seeds underneath it. Similarly, Ruwanza (2019) reported increased species diversity underneath three nurse plants in old fields, although diversity varied with growth form, e.g., trees and shrub counts were more underneath nurse plant canopy than outside, yet graminoids showed the opposite trend. A possible explanation for why the diversity of other plant species was high under *V. karroo* nurse plants is the plant–plant facilitation theory that has been reported in previous studies (Navarro-Cano et al. 2019). Several studies have shown that nurse plants have a positive association with surrounding plants, implying that other plants benefit from nurse plants (Brooker et al. 2008; Navarro-Cano et al. 2019). Brooker et al. (2007) reported that plant–plant facilitation can result in enhanced growth, reproduction and survival of species that are benefiting from proximity to other plants. Navarro-Cano et al. (2019) used the term ecosystem engineers to refer to nurse plants that facilitate the establishment of other species. These ecosystem engineer plants also called nurse plants have stress-tolerant traits that allow them to establish easily and support surrounding plants. For example, they provide other plants with canopy shade, moist soils underneath them, and create nutrient-rich microsites that benefit other plants (Graff & Aguiar 2017; Navarro-Cano et al. 2019). Besides creating conducive environments to facilitate the growth of other plant species, nurse plants also reduce abiotic and climatic stress for other plants e.g., temperature reduction through shade provisioning (Callaway 2007).

Besides the dominance of *V. karroo* seedlings underneath the nurse plant, six species, namely *Searsia crenata, Azima tetracantha, Amaranthus* sp., *Asparagus africanus, Bulbine* sp. and *Opuntia* sp., had frequency occupancy of more than 50% under nurse plants. The dominance of these species could be linked to several factors such as competition-related co-occurrence with nurse plants, shade tolerance and invasion traits. Shade-tolerant species need to have specific traits, such as the ability to tolerate limiting factors such as light (Valladares & Niinemets 2008) to survive under nurse plants. It is possible that shrub species such as *S. crenata* have traits that allow it to grow in the shade of other plants, since the plant species can tolerate harsh conditions such as drought and frost. For some plant species, such as *Asparagus africanus*, the ability to propagate both sexually and clonally (vegetatively) could explain its dominance underneath nurse plants. Yang and Kim (2016) suggested that perennial plants tend to favour clonal reproduction under favourable soil nutrients and moisture habitats, conditions that we also observed under *V. karroo* nurse plants. For *Opuntia* species, its invasion traits, such as being adaptable to different environmental conditions and can survive better in degraded conditions, such as old fields (Sipango et al. 2022) could explain its high frequency occupancy underneath *V. karroo* nurse plants. A study by Novoa et al. (2021) reported that *O. stricta* germinated well on soils conditioned by the native plants *V. nilotica* and *Spirostachys africana* than on soils from open patches. The above-mentioned results seem to suggest that nurse plants create conditions for the establishment of other plants, such as the invasive *Opuntia* species. In contrast, the above-mentioned study also reported that *O. stricta* can nurse other plants, implying that *Opuntia* species can co-occur with other plants.

Our observed vegetation and soil results seem to suggest a positive plant–soil feedback that could explain the dominance of other plants underneath nurse plants. Facilitation-driven cascade systems associated with nurse plants have been reported in the past (Navarro-Cano et al. 2019), where surrounding plants benefit from the nurse plant and the benefits impact soil communities through nutrient cycling and microbial decomposition (Navarro-Cano et al. 2019). In turn, below ground nutrient and microbial benefits promote ecosystem feedback that will benefit the nurse plant and the subcanopy plant community, resulting in increased abundance and diversity. Therefore, plant-soil feedback underneath nurse plants can explain the observed diverse and abundant species under compared to outside nurse plants (Clewell et al. 2005; Navarro-Cano et al. 2018).

Conclusion and recommendations

This study highlights the role and importance of *V. karroo* nurse plant in old fields targeted for passive ecological restoration. We reported improved soil properties such as soil C, N, Ca, Mg and penetration resistance, as well as the dominance of native vegetation under the nurse plants. Both the improved soil properties and the presence of diverse vegetation underneath nurse plants are indications that *V. karroo* plays a positive facilitation role that could be crucial to ecosystem recovery in these degraded old fields. These results support our prediction that the nurse plant *V. karroo* facilitates soil and vegetation recovery in old fields targeted for passive restoration. Based on these results, we conclude that *V. karroo* has the potential to act as an ecosystem engineer that could facilitate plant and soil recovery in these old fields. However, *V. karroo* is a well-known bush encroacher that has invasive and expansion traits (Dingaan & Du Preez 2018). Its removal for bush encroachment management purposes should therefore consider: (i) selective removal of *V. karroo* plants that do not provide refugia for underneath vegetation; (ii) removal should be done in a way that protects underneath surrounding vegetation (i.e., remove young rather than older *V. karroo* individuals); and (iii) protect, through fencing, some *V. karroo* plants to reduce the browsing of subcanopy species by mesoherbivores. The successful protection of *V. karroo* as a nurse plant in old fields has the potential to accelerate soil and vegetation recovery during passive restoration in these regions.

Acknowledgements

Thanks to the National Research Foundation (NRF: research grant UID number 137789) for funding to conduct fieldwork. Also, thanks to the Department of Environmental Science at Rhodes University for providing equipment and transport for fieldwork. We also thank Messrs Uzziah Mutumbi and Tafara Frank Bute, who assisted with fieldwork. We are grateful to the owners, managers and research coordinators at Tanglewood research farm, specifically Peter Chadwick, William Fowlds and Richard Smithers for permission to conduct this study and logistical help during fieldwork.

Competing interests

The authors declare that they have no financial or personal relationship(s) that may have inappropriately influenced them in writing this article.

Authors' contributions

S.R. (Rhodes University) was the project leader and V.M. (Rhodes University) was the student. S.R. and V.M. were responsible for experimental and project design. V.M. performed most of the experiments and collected the data. Both S.R. and V.M. made conceptual contributions. V.M. prepared the samples for analysis. S.R. conducted data analysis and wrote the first draft of the manuscript. V.M. reviewed the draft manuscript.

Funding

This research was funded by National Research Foundation (NRF) South Africa, under the programme NRF Research Development Grant for Y-Rated Researchers (Grant number 137789).

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BOTHALIA – African Biodiversity & Conservation
ISSN: (Online) 2311-9284, (Print) 0006-8241

A pollination mutualism over the edge: growth form and fig traits respond differently during niche expansion to arid environments

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Dates
Submitted: 2 August 2023
Accepted: 6 June 2024
Published: 19 August 2024

How to cite this article:
McLeish, M.J., Guo, D. & Van Noort, S., 2024, 'A pollination mutualism over the edge: growth form and fig traits respond differently during niche expansion to arid environments', *Bothalia* 54, a9. http://dx.doi.org/10.38201/btha.abc.v54.9

Background: It is unclear how climate shifts may interfere with the diversification of tightly associated species interactions. Obligate pollination mutualisms are ideal for investigating the underlying processes of niche evolution by environmental change.

Objectives: Niche evolution that corresponds with phenotype-by-environment interactions that include climate shifts is expected to affect the stability of partner associations of mutualisms. Here, we compare the evolution of fig syconium size and growth form strategies for coping with soil water stress during a range expansion by *Ficus* into arid environments.

Methods: Niche models of 31 *Ficus* taxa were used to define contemporary habitat requirements of each species, which are then incorporated into Bayesian mixed models to examine the response of each trait to the soil water variables, other environmental variables and phylogenetic dependencies.

Results: The results showed that phylogenetic constraints best explained syconium size variation, while environmental lability best characterised growth form variation. Two species adapted to arid environments that exhibited convergence in these traits had significantly different habitat requirements compared to forest and savanna species.

Conclusion: The niche expansions by *Ficus ilicina* and *Ficus cordata* involved distinct historical processes. The findings suggest selection for traits that varied at different temporal scales limit the rate of niche expansions, and potentially destabilise mutualist partnerships and promote host shifts.

Keywords: phenotype-by-environment, habitat selection, ecological niche, water stress, Karoo, phylogenetic constraints, host shift.

Introduction

Abiotic and biotic factors limit the geographical ranges of all species, but also create opportunities for their diversification (Ackerly 2003; Holt 2009; Carscadden et al. 2020; Mestre et al. 2020). However, climate shifts potentially reorganise species phenotypes, the geographic distributions of resources, and drive niche evolution of respective partner species of mutualisms (Joy 2013; Werner et al. 2018). Phenotype-by-environment interactions (Via & Lande 1985) that are critical to the contemporary geographic distribution of mutualisms are rarely linked to their evolutionary histories during niche and climate shifts. Plant growth form responds to changes in the abiotic environment and has consequences for physiological innovations of the plant (Rowe & Speck 2005). Specifically in *Ficus*, syconium morphology influences the reproductive ecology of the fig–fig wasp mutualism through the availability of female florets used as wasp breeding sites, and the number of seeds that can be produced by the tree (Bronstein 2001). Ecological or evolutionary mismatches in these traits might underlie host shifts and the exceptions to the extraordinary patterns of co-diversification observed in the *Ficus* pollination mutualism.

Species associations that exhibit strong evolutionary constraints (i.e., the observed pattern as generated by prior evolution) may either limit (Bronstein 2001) or facilitate (Joy 2013) processes such as niche expansions by which mutualisms diversify (Gilman et al. 2011; Burkle et al. 2013). Theory predicts that when species interactions of mutualisms are compartmentalised, when there is high interaction specificity, they are susceptible to destabilisation (Thébault & Fontaine 2010; McLeish et al. 2011). Niche expansions may cause phenotypic and phenological mismatches that destabilise interactions between partners and determine avenues of diversification or extinction. Generally, it is uncertain how selective pressures act on respective pairs of a mutualism because each species need not express the same functional associations with the environment (Sachs & Simms 2006; Ibanez et al. 2016). For instance, if phenotype-by-environment interactions are strong, population divergence may occur along resource gradients during environmental change over time, and reorganise underlying genotypes critical to functional aspects of species associations (Bolnick et al. 2011; Newman et al. 2012). Populations experiencing changes to environmental conditions that result in low-density geographic distributions, are expected to alter the ecological niches of respective mutualist partner species (e.g., Gilman et al. 2011). This can potentially lead to other association types or to the extinction of one or both partners (Kiers et al. 2010). Species that are distributed on the range limits, in marginal environments, or are subject to climate shifts may exhibit these demographic processes (Bridle & Vines 2007).

Obligate pollination mutualisms are ideal for investigating the underlying processes of niche evolution when responses to environmental perturbations are expected to be different between free-living and sedentary partner species of insect–plant associations. The spectacular co-diversification pattern inferred between *Ficus* and their pollinator fig wasps (Agaonidae, Chalcidoidea) suggests that their co-evolution has been contributed to by phylogenetic constraints (Van Noort & Compton 1996; Cornille et al. 2011). By phylogenetic constraint, we refer to the importance of ancestry as a strong determinant of the *Ficus* species that a wasp will obligately pollinate (Hawkins & Compton 1992). The growing number of exceptions to these mirrored patterns of diversification are indicative of non-phylogenetic influences (Renoult et al. 2009; Cruaud et al. 2011; McLeish & Van Noort 2012) and suggest environmental variation may have influenced the reproductive ecology, stability or diversification of the mutualism.

In South Africa, *Ficus* largely occurs as mono-specific patches in savanna or coexists in forest habitats. However, some species have adapted to arid environments and water-stressed habitats. The observation that *Ficus* species occupy arid habitats raises the question of how they evolved to expand out of their pantropical ranges (Cruaud et al. 2012), and how this may have influenced the reproductive ecology of the mutualism. Both growth form and syconium morphology are associated with strategies for coping with water stress and are hypothesised to be sensitive to water availability gradients (Piedra-Malagón et al. 2011). Plant growth form responds to changes in the abiotic environment and has consequences for physiological innovations of the plant (Rowe & Speck 2005). For example, the evolutionary labile expression of growth form in *Ficus* species has a direct influence on the assimilation of water (Hao et al. 2011), and water loss from their syconia (Patiño et al. 1994). For example, Hao and colleague's (2010) work on leaf structure and physiological traits associated with growth form and habitat show trade-offs between leaf water flux and leaf drought tolerance. The correlation between syconium diameter and leaf area has also been shown to respond to environmental variation (Lasky et al. 2014). Variation in physiological tolerances has a critical role in the geographical distributions and associations of host figs and their pollinators (Warren et al. 2010). Syconium morphology influences host and pollinator fitness because of the duality between the availability of female florets in the syconium that are galled and used as breeding sites, and the number of seeds that can be produced by the tree (Bronstein 2001). Additionally, syconium size is critical to maintaining non-lethal internal temperatures within the tolerance thresholds of pollinating fig wasps (Patiño et al. 1994). In tropical habitats, large syconia are critical to the survival of wasps and the regulation of internal temperature that is dependent on transpirational cooling and optimisation of water resources (Krishnan et al. 2014). Thus, growth form and syconia trait adaptations may differ between environments with contrasting water resource availability. Most *Ficus* species in subgenus *Urostigma* have a hemi-epiphyte habit with a growth stage resistant to water deficiencies of the canopy environment before the transition to the terrestrial stage, and are pre-adapted to an epilithic growth form (lithophyte) in drier environments (Berg & Corner 2005; Hao et al. 2010). Hemi-epiphytism has evolved independently on multiple occasions and is expected to have undergone selection for drought tolerant traits (Hao et al. 2011). We expected that soil water gradients influenced contemporary and historical geographical distributions of growth form and syconium size of *Ficus* in South Africa. Changes to the distribution of these traits during niche expansions may have destabilised mutualist associations and resulted in host shifts evident in many South African lineages (McLeish & Van Noort 2012).

In this study we aim to test whether the geographic distribution of fig traits central to the physiological tolerance thresholds and reproductive biology of the fig pollination mutualism, corresponded to either environmental variation or phylogenetic constraints. Soil water properties have a strong relationship with niche differentiation of species at local and much larger spatial scales (Guo et al. 2017) and were used in conjunction with other environmental variables to connect climate to topographic variation in moisture availability (Larcher 2003). We test the hypotheses that: 1) physiological and reproductive trait responses correspond to environmental variation, or 2) to phylogenetic constraints. We first use habitat selection analyses to describe each *Ficus* species' soil water resource and ecological niche dimensions and use these as predictors of trait variation and test phylogenetic dependencies. Habitat selection in plants is an evolutionary process involving the adjustment of species' geographical ranges by environmental factors (Bazzaz 1991). Second, we examine the relationship between variation in growth form and syconium traits with soil water and environmental variation while correcting for phylogenetic dependencies using Markov chain Monte Carlo generalised linear mixed models (MCMCglmms). We test the hypothesis that the evolution of growth form and syconium size of *Ficus* covaried with soil water and environmental variation. By evaluating habitat requirements of *Ficus* (Moraceae) in South Africa, we investigate whether the evolutionary histories of physiological tolerance and reproductive traits corresponded with each other during niche expansions by ancestral lineages of *F. ilicina* and *F. cordata* from hydric to xeric climates. The findings showed that the occupancy of the Karoo deserts by *F. ilicina* and *F. cordata*, corresponded with convergence in traits but via distinct evolutionary histories. Generally, stronger niche conservatism in syconium size contrasted the environmental lability of growth form and suggested that interdependencies between these traits may limit the rate of niche expansions.

Materials and methods

Species biology

Approximately 500 of the 800 or so *Ficus* species germinate as epiphytes and develop into hemi-epiphytes that rely on a host for physical support (Berg & Corner 2005). Hemi-epiphytic forms of *Ficus* predominate in tropical environments, while free-standing trees (i.e., arborescent) and lithophyte forms are associated with drier environments at higher latitudes at the extents of circum-tropical ranges (Berg & Wiebes 1992; Dixon 2003). The fruit-like structure that *Ficus* species produce, develop as syconia and provide a keystone resource for a rich assemblage of pollinating and non-pollinating wasps, and many other invertebrate and vertebrate species (Compton & Van Noort 1992). Asynchronous production of syconia throughout the year requires continuous cycling of pollinators between patches to maintain viable populations of both mutualistic partners. Heterogeneous host distributions make dispersal of fig wasps among patches risky and exposes them to desiccation especially in dry environments.

Habitat selection analyses

To define the habitat requirements of *Ficus* and conduct habitat selection analyses (Dolédec 2000; Calenge 2006), we extracted environmental variables from raster data that were then associated with presence records of each taxon. The method provides an estimate called marginality, which corresponds to deviations of a species mean resource requirements from the mean conditions of the entire study area. The method was used to generate environmental predictors for use in the prediction of trait variation (see below). The variables used in the habitat selection analysis comprised soil water stress (SWS) that indicates the number of days per year at which soil water content would be critical to plant stress (Schulze et al. 2007). Areas inside the arid west of South Africa are typically exposed to severe soil water stress (SWS) for at least 150 days of the year and can be for periods of more than 300 days. Plant available water (PAW) was also used to indicate variation in the storage of water available from the soil profile (Schulze et al. 2007). Both SWS and PAW depend on soil texture and the soil profile depth (Supplementary material S1). We also included variables that influence soil quality, drainage and evapotranspiration. These comprised elevation (https://srtm.csi.cgiar.org/srtmdata), slope, aspect (calculated from elevation) and biome class (https://bgis.sanbi.org/SpatialDataset/Detail/329). Biomes are classified according to vegetation types defined by contributions of dominant, common and rare species, in conjunction with topographic and climatic features (Dayaram et al. 2017, Mucina & Rutherford 2006). Biome categories generalise about climatic zonation and bio-productivity that potentially constrain each species distribution. We used a modification of the outlying mean index (OMI) approach called canonical OMI (canOMI) in the habitat selection analyses, to evaluate soil water resource requirements and environmental dimensions of each species. The canOMI approach corrects for potential biases created by the presence of strong environmental patterns characteristic of South Africa and transforms the sampling area into resource units.

Presence data of 2 163 localities comprising 1 202 unique records of 31 *Ficus* species and subspecies in South Africa (Supplementary Table S1) were compiled from field trip collections and the SANBI and PRECIS databases (available at https://posa.sanbi.org/sanbi/Explore). The presence data represented approximately 75% of known South African species. The PRECIS data included records that synonymise *F. petersii* and *F. burkei* as *F. thonningii*. We retained the taxonomy used in these records for consistency and assume that this will result in *F. thonningii* having resource use characteristics similar to the other two species. Species with low sample sizes of < 3 individuals (i.e., *F. natalensis* subsp. *graniticola* and *F. sycomorus* subsp. *gnaphalocarpa*) were retained after pilot analyses indicated their inclusion resulted in negligible changes to niche comparisons and the MCMCglmm outcomes. We treated records with subspecies assignments as separate taxa in the habitat selection analyses and tested the effect of synonymising them in the MCMCglmm analyses. The approach assumes uniform sampling effort and probability of detection among species and is addressed by weighting the sampling units in proportion to their abundance. Each resource unit corresponds to a pixel of a raster map and the soil water variables associated with it. The canOMI analysis was conducted using the R version 3.6.3 (R Core Team 2012) package *adehabitatHS* (Calenge 2006).

Phylogenetic dependencies

To estimate phylogenetic dependencies in the prediction of growth form and syconium size, an ultrametric consensus phylogeny of 37 species (alignment available from authors on request) was pruned to 24 South African species for which there were corresponding presence records. As there were sequences available for taxa identified to species and subspecies level (*F. cordata* and *F. cordata* subsp. *cordata*), both were retained in the interest of inclusivity and sample size. We used MRBAYES 3.1.1 (Huelsenbeck & Ronquist 2001) to evaluate phylogenetic uncertainty and BEAST and BEAUTI v. 1.7.5 (Drummond et al. 2012) to infer an ultrametric consensus tree. Sequence data of up to 767 bp of a ribosomal internal transcribed spacer (*ITS*) and up to 479 bp of external transcribed spacer (*ETS*) were compiled from various sources (Jousselin et al. 2003; Rønsted et al. 2007; McLeish & Van Noort 2012). All sequence data are available from the GenBank repository (https://www.ncbi.nlm.nih.gov/genbank/). The sequence data was partitioned by *ITS* and *ETS* loci, and a general time reversible DNA substitution model (GTR) with gamma distributed (+G) rates and a proportion of invariant sites (+I) applied for the analysis. Four Markov chains were run for 40 million generations, sampling each chain every 1 000 trees. Posterior probabilities and mean branch lengths were derived from 35 000 post-burnin trees. Convergence and posterior parameter distributions were assessed using the MCMC Tracer Analysis Tool v.1.6 (Rambaut et al. 2014). An inverse relatedness matrix and phylogenetic covariance matrix were generated from the consensus tree using the R package *MCMCglmm* (Hadfield & Nakagawa 2010) and introduced to the MCMCglmms as a random variable (Supplementary material S2).

Trait response models: MCMCglmms

We evaluated the relative strengths of PAW and SWS in predicting growth form and fig size with and without the contributions of the other topological variables (altitude, aspect, slope and biome), to assess the effect of variables on model performance (Table 1). The Bayesian mixed model approach was selected because it allows the analysis of phylogenetic dependencies using categorical (growth form) and continuous (syconium size) response variables. Species-level variation in syconium size was based on diameter measurements sourced from the literature (Berg & Wiebes 1992; Burrows & Burrows 2003). We calculated a mean value of syconium diameter for each species to infer variation across the internal nodes of the phylogeny, as this parameter is appropriate for testing the effects of ancestry on phylogenetic dependencies (e.g. Ackerly et al. 2006). We coded growth form for each species as a multinomial variable for lithophyte, terrestrial tree, hemi-epiphyte or combinations of these categories (Supplementary Table S2). For tests of phylogenetic dependencies, we aggregated each subspecies of (*F. cordata*, *F. natalensis*, *F. polita*, *F. sansibarica*, *F. sycomorus* and *F. tremula*) to a

Table 1. Mixed model (MCMCglmms) designs showing response traits and predictor variables; PAW = plant available water; SWS = soil water stress

Response trait	Predictor variables [random factor]
Syconium size	PAW + SWS + [phylogeny + species]
Syconium size	mean PAW + within-species PAW + mean SWS + within-species SWS + [phylogeny + species]
Syconium size	PAW + SWS + elevation + slope + [phylogeny + species + biome + aspect]
Growth form	PAW + SWS + [phylogeny + species]
Growth form	mean PAW + within-species PAW + mean SWS + within-species SWS + [phylogeny + species]
Growth form	PAW + SWS + elevation + slope + [phylogeny + species + biome + aspect]

single species to correspond with the phylogeny. A random factor (taxon) that distinguished all taxa including subspecies, was used to test the effect of aggregating subspecies in the MCMCglmms. Variables for biome and aspect were treated as categorical random factors. The remaining variables were assessed for normality and treated as continuous normal predictors. Slope was square root transformed and all variables scaled (subtracting the mean and dividing the result by the standard deviation) for the MCMCglmm analyses (R code available from authors on request).

To evaluate the level of species-specificity of the soil water variable, we assessed the proportion of within- and between-species variance using MCMCglmms. Species mean PAW and SWS were included as fixed factors to assess between-species variance, in addition to fixed factors for the individual estimates of PAW and SWS to look at within-species variance. A random factor for species was included in addition to one for phylogeny to accommodate the modelling of between-species contributions. Finally, phylogenetic heritability (the probability associated with an ancestral state), H^2, of growth form and syconium size was calculated as $\sigma^2_a / (\sigma^2_a + \sigma^2_e)$, where σ^2_e is the residual variance (comprising the fixed effects) and σ^2_a is the phylogenetic variance. The MCMCglmms of species-specificity and the heritability analyses were both run for 10.0×10^6 iterations with a thinning interval of 1 000 and burnin of 10 000. We used a *G*-structure prior of $V = 1$ and $nu = 0.002$, and a *R*-structure prior of $V = 1$ and $nu = 1$ in the syconium size model. For the growth form model, we used a *G*-structure prior of $V = 1$, and $nu = 1\,000$ for random variables and a fixed *R*-structure prior ($fix = 1$) at $V = 200$. The growth form data were from a categorical variable distribution, and therefore, residual variance was fixed (i.e., to an arbitrary prior). The posterior distribution of predictor variables (Sol), covariance estimates (VCV), and autocorrelation between posterior values sampled from the Markov chain were assessed in all models to ensure parameter convergence and a reasonable approximation of the true posterior. The Bayesian *p*-value (*pMCMC*) is (2×) the proportion of values from the posterior estimate that are of the opposite sign to the parameter calculated from the Monte Carlo sampling and provides a way to assess variable support. The estimate is credible if its highest posterior density (HPD) distribution does not span zero. All MCMCglmm analyses were conducted using the R package *MCMCglmm*.

Results

Habitat selection analyses

The analyses of habitat selection that included all predictor variables shows three main patterns: (i) the subspecies of *F. cordata* and *F. ilicina* cluster along the soil water variables vectors and with Karoo, Thicket, Fynbos and Grassland biomes (Figure 1, Figure 2a); (ii) most species clustered between the vectors for PAW and Savanna; (iii) and there were three species, *F. bizanae*, *F. natalensis* and *F. polita* that were strongly affiliated with high PAW and the Forest biome (Figure 2a). Kruskal-Wallis rank sum tests indicated that syconium size ($\chi^2_{(15)} = 14.798$, $p = 0.046$) and growth form ($\chi^2_{(6)} = 18.307$, $p < 0.006$) were significantly associated with the first axis of the canOMI analysis, and indicated that both traits had a strong relationship with contemporary water resource variables. The first canOMI analyses indicated *F. cordata* and *F. ilicina* occupied biomes that represent atypical distributions of *Ficus* in South Africa, i.e., lithophyte species that have shifted towards south-facing slopes, higher SWS, and lower PAW in the Karoo biomes. A majority of species occupy the Savanna biome, with comparatively few Forest biome species. The results of a second canOMI analysis that comprised PAW and SWS only, differed from the analysis that comprised all variables, as it showed that biome had a strong influence on the forest species (Figure 2b). Otherwise, the same general patterns were maintained between the two analyses. Both showed that the obligate lithophyte species were clearly distinguished from the other species (the second canOMI analysis). For instance, the differences in the mean PAW and SWS resource unit distributions used by and available to *F. cordata* and *F. ilicina* were opposite to the savanna and forest species (Figure 3). *Ficus cordata* and *F. ilicina* belong to distantly related *Ficus* sections yet converged on the same ecological strategies; both had similar moisture requirements, are epilithic and produce small syconia.

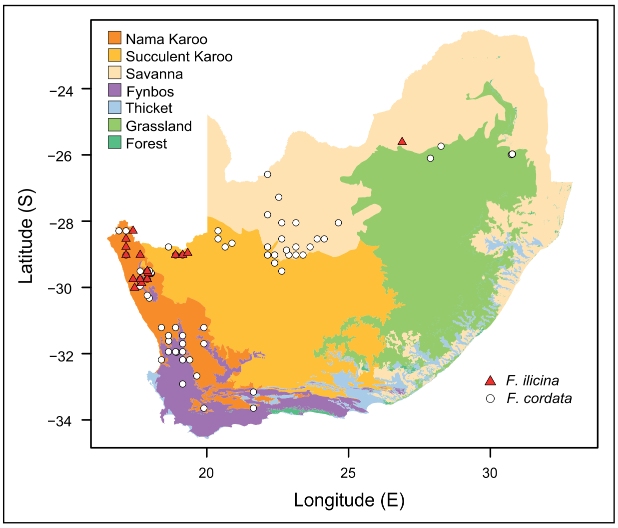

Figure 1. South African biomes and the distributions of *Ficus ilicina* and *Ficus cordata*. Biomes are classified according to vegetation types defined by contributions of dominant, common and rare species, in conjunction with topographic and climatic features.

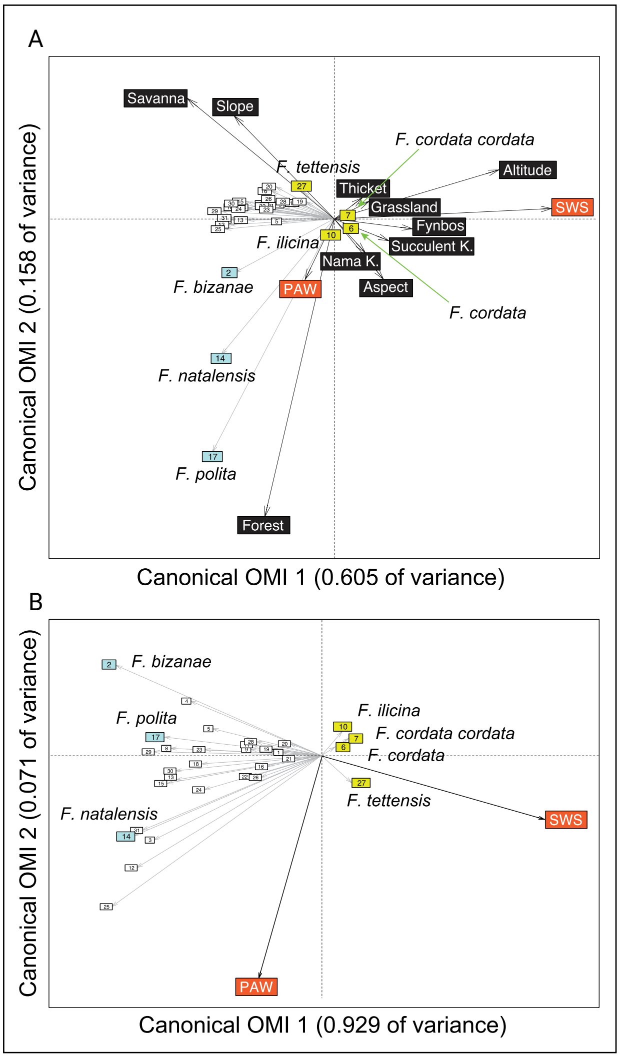

Figure 2. The first two axes of canonical outlying mean index (OMI) analyses including all environmental variables (a) and only soil water stress (SWS) and plant available water (PAW) variables (b). Highlighted are obligate lithophytes *F. cordata*, *F. ilicina*, *F. tettensis* and 'outlier' species. Vectors for each environmental layer are superimposed over the marginal vectors for each species. Numeric species codes are given in Supplementary Table S1.

Consensus phylogeny

To visualise phylogenetic and trait relationships among species caused by shared ancestry, a consensus was inferred. The consensus phylogeny (Figure 4) indicated good stem clade posterior probability support (0.93–1.00) and generally good crown clade support (0.83–1.00) that was consistent with the topology of a recent study (Cruaud et al. 2012). The distribution of growth form across the terminal branches indicated phylogenetic clustering of obligate terrestrial tree species. However, the obligate lithophytes were phylogenetically over-dispersed with *F. tettensis*–*F. abutilifolia*, *F. salicifolia*–*F. cordata* and *F. ilicina* belonging to three different *Ficus* subsections and indicated multiple evolutionary origins of this trait. Syconium size was phylogenetically conserved in subsection *Caulocarpae*, *Sycomorus* and *Urostigma*, compared to greater variation in *Chlamydodorae* and *Platyphyllae*. The consensus tree inferred that the relationship between the traits tended to be clustered only in sections *Sycomorus* and *Urostigma*, with the large syconia produced by obligate trees, and the small syconia by obligate lithophytes, respectively.

Trait evolution and soil water gradients

We inferred a phylogeny to correct for dependencies among species caused by shared ancestry, using Bayesian trait reconstructions implemented with MCMCglmms. As SWS and PAW were estimated multiple times for each species, we assessed between- and within-species variance. The analyses indicated weak ($pMCMC > 0.962$) species-specific variance compared to strong interspecific differences ($pMCMC < 0.046$) in both growth form and syconium size (Supplementary Table S3), indicating relatively high interspecies variation. We weighted variance priors for the *G*- (phylogeny) and *R*- (residual) covariance structures to evaluate phylogenetic dependencies and used the DIC (Deviance Information Criterion) to compare model-fit (Supplementary Table S4). Mean syconium size was best explained when the bias favoured the random factor for phylogeny (Δ-DIC = 3 553.5). By contrast, growth form was best explained when the priors favoured the residual over the phylogenetic variance component (Δ-DIC = -275.7). The variance contributions by phylogeny to syconium size relative to growth form indicated that phylogenetic dependencies were a stronger factor in the evolution of syconium size compared to growth form.

The MCMCglmms of soil water, environmental and trait variation, indicated the effects of SWS ($pMCMC < 0.001$) and PAW ($pMCMC = 0.002$) on growth form were strong relative to the weak effects of SWS ($pMCMC = 0.600$) and PAW ($pMCMC = 0.697$) on syconium size (Table 2). The inclusion of the other environmental predictors (Supplementary Table S5) improved fit in the growth form model (Δ-DIC = 5.72) but reduced fit in the syconium size model (Δ-DIC = -9.9). These contrasts in model-fit indicated that growth form, relative to syconium size, responded better to the other environmental predictors than explained by PAW and SWS alone. The heritability analyses indicated that syconium size had a high probability (i.e., 95% CI = 95% Credible Interval) of being transmitted to descendants (0.980 with 95% CI of 0.966–0.994) compared to growth form (0.005 with 95% CI of 0.005–0.006). Together, the MCMCglmm analyses indicated that the distribution of growth form in South Africa was strongly affected by soil water gradients relative to syconium size that had a much stronger phylogenetic signal.

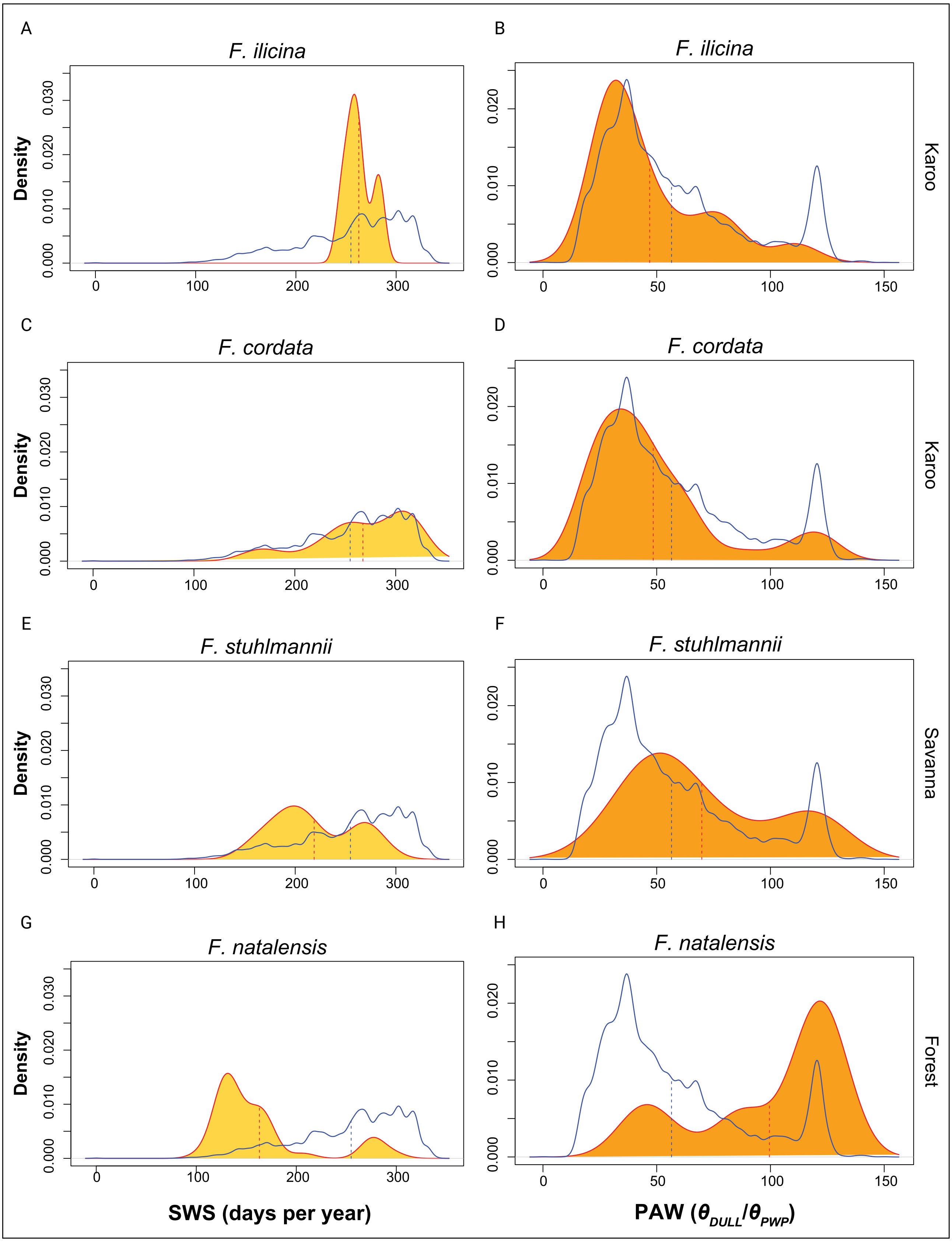

Figure 3. Kernel density estimation of available (smoothed line) and used resource units (filled distribution) of arid, savanna and forest species. The mean of each distribution is indicated by dashed lines. Soil water stress (SWS) indicates the number of days per year at which soil water content would be at critical plant stress. Plant available water (PAW) is the ratio of the drained upper limit of soil water (θ_{DUL}), and the permanent wilting point of soil water (θ_{PWP}). Available units (environment) are sites that correspond to where a species presence is uncertain, but where we consider that it could be present as characterised with the soil water variables.

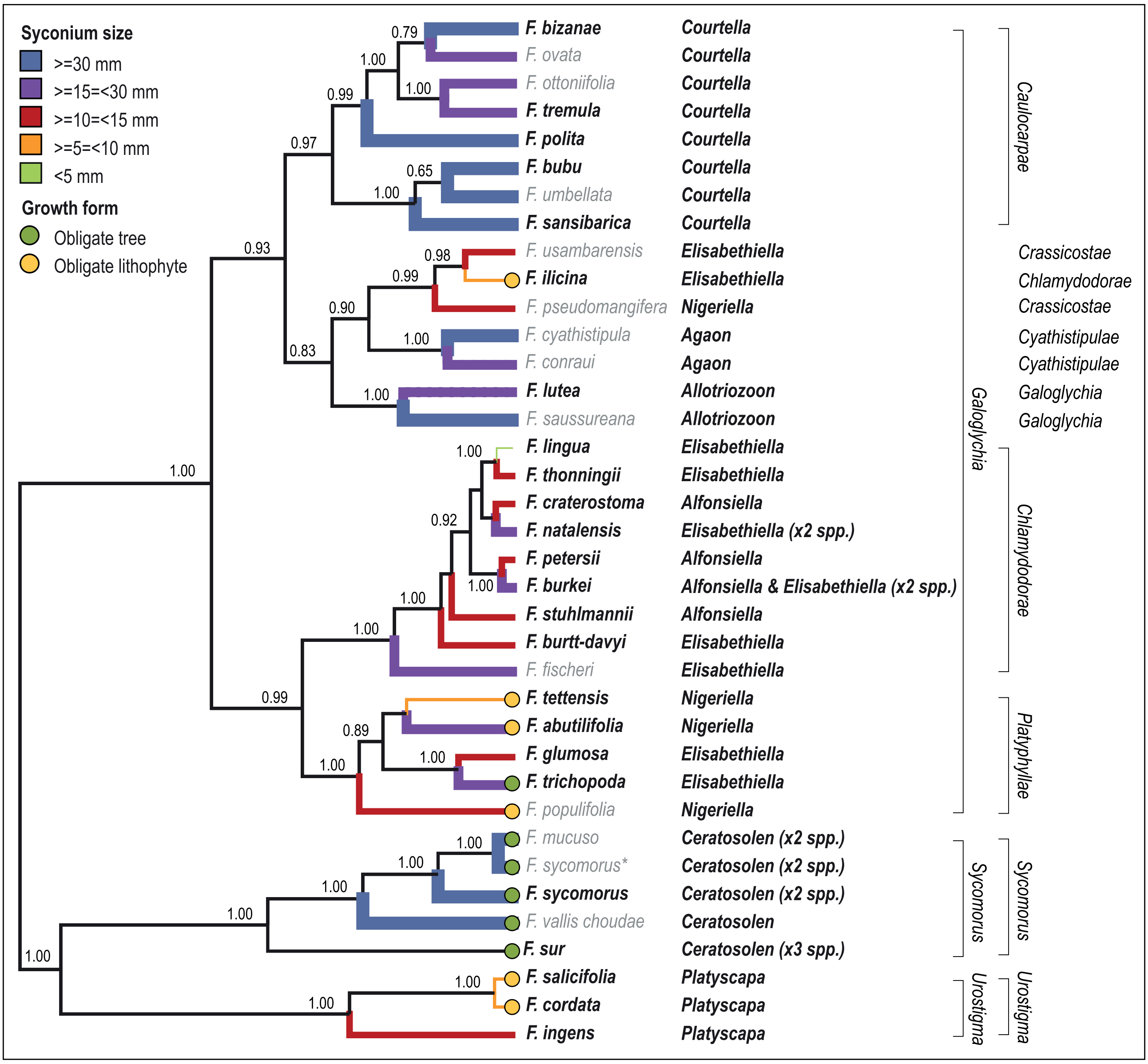

Figure 4. A Bayesian consensus chronogram of *Ficus* species in Africa. The taxa pruned for the MCMCglmm analyses have grey terminal taxon labels. Circles on terminal branches indicate obligate lithophytes or obligate terrestrial trees with unlabelled terminals as having multiple growth forms (see Supplementary Table S2 for details). Branch weight corresponds to mean syconium size. Posterior probabilities indicated on the branches. The respective associated fig wasp pollinator genera are indicated in the adjacent column to the host fig species. *Ficus* sections and subsections indicated respectively by vertical bars on the right. *Ficus ovata* has become a synonym of *F. laurifolia*. *Sequence data from *F. sycomorus* sampled in the Congo basin.

Table 2. The posterior distribution of the MCMCglmm coefficients for growth form and mean syconium size responses as explained by PAW (plant available water), SWS (soil water stress), and phylogeny. CI = 95% Credible Interval. Strong effects indicated with bold *pMCMC* value. The term *G* describes a covariance matrix of the random effects, and *R* as the covariance matrix of the residual variances. The Bayesian p-value (*pMCMC*) is (2×) the proportion of values from the posterior estimate that are of the opposite sign to the parameter calculated from the Monte Carlo sampling and provides a way to assess variable support

	Variable	Posterior mean	Lower CI	Upper CI	Effective sample	*pMCMC*
Syconium size						
G-structure	Phylogeny	2.087	1.061	3.559	990	-
	Taxon	0.007	0.000	0.025	990	-
R-structure	Residual	0.029	0.021	0.038	1202	-
Fixed effects	PAW	-0.028	-0.167	0.103	990	0.697
	SWS	-0.063	-0.289	0.162	990	0.600

Table 2. The posterior distribution of the MCMCglmm coefficients for growth form and mean syconium size responses as explained by PAW (plant available water), SWS (soil water stress), and phylogeny. CI = 95% Credible Interval. Strong effects indicated with bold *pMCMC* value. The term *G* describes a covariance matrix of the random effects, and *R* as the covariance matrix of the residual variances. The Bayesian p-value (*pMCMC*) is (2×) the proportion of values from the posterior estimate that are of the opposite sign to the parameter calculated from the Monte Carlo sampling and provides a way to assess variable support (continued)

	Variable	Posterior mean	Lower CI	Upper CI	Effective sample	*pMCMC*
Growth form						
G-structure	Phylogeny	1.088	0.983	1.197	990	-
	Taxon	1.154	1.051	1.267	990	-
R-structure	Residual	200	200	200	0*	-
Fixed effects	PAW	2.848	0.996	4.798	1092	**0.002**
	SWS	-12.519	-14.235	-10.692	990	**< 0.001**

*Fixed variance prior for categorical response.

Discussion

We linked the soil water requirements of *Ficus* species with the geographic distributions and evolutionary histories of growth form and syconium size. The significant relationships between the water-stress predictors and trait variation agreed with the hypotheses that *Ficus* traits are sensitive to water availability gradients (e.g., Piedra-Malagón et al. 2011). However, the growth form responses to soil water variation were stronger than those of syconium size in explaining the evolution of these traits. The strong phylogenetic signal of syconium size in concert with their consistent spatial positioning on the tree within the respective subsections contrasted with that of growth form, and supported the hypothesis that syconium morphology is crucial to the reproductive biology and stability of the mutualism (Compton & Van Noort 1992). Our findings indicated that constraints on syconium size evolution might have limited the rate of expansion by *Ficus* to arid environments, while the environmental lability of growth form may have facilitated niche evolution. Such performance trade-offs that arise due to complex patterns of covariation among functionally related traits (Pigliucci 2003) might have a role in destabilising mutualistic associations with pollinators.

Figs and soil water gradients

Our findings supported the hypothesis that the contemporary distribution of both traits corresponded to water gradients (i.e., canOMI axis one) in South Africa. For instance, *F. ilicina* and *F. cordata* are two obligate lithophyte species with small syconia, which occupy particularly low PAW and high SWS habitats (Figures 2 and 3) in the Nama and Succulent Karoo deserts (Figure 1). The habitat selection analyses distinguished the contemporary distributions of these species from the majority of the other *Ficus* lineages in South Africa that occupy the Savanna biome. For instance, *F. cordata* and *F. ilicina* were more frequently observed on southward-facing aspects that presumably resulted in lower exposure to solar radiation. Conversely, evidence of occupation on northward-facing aspects in a large majority of the other species suggests an advantage in increased exposure during colder months in seasonal climates. Climate shifts during the Quaternary caused changes to water availability in southern Africa and resulted in the dominance of arid-adapted vegetation typical of the savanna biomes today (Linder 2014).

A number of processes may have led to the occupation of arid environments by *F. ilicina* and *F. cordata*. For example, covariance among phenotypes might have arisen due to environmental filtering (i.e., ecological sorting) that occurs due to spatial autocorrelation (Freckleton & Jetz 2008). Alternatively, the coexistence of these distantly related species may have arisen as a consequence of allopatric speciation between ecologically similar habitats, with subsequent range shifts into sympatry in their contemporary distributions. Although there was evidence of 'selection' for higher SWS in both the lineages, *F. ilicina* occupied habitats with relatively narrow SWS variation (Figure 3) compared to *F. cordata*, which might indicate alternative routes to adaptation to water stressed habitats. For example, it has been shown that in seasonal semideciduous forest in Brazil, hemi-epiphytes established at much lower height on host trees than in evergreen rainforests (Coelho et al. 2014). The distinctions in environmental niche requirements between the arid-distributed species and the other obligate lithophytes that occupy savanna (*F. abutilifolia*, *F. salicifolia* and *F. tettensis*), suggests a number of unique historical factors influenced the occupation of water-stressed habitats by ancestral lineages of the obligate lithophyte species. Both the arid-adapted species have relatively restricted distributions from southwestern Angola through the Namib Desert into South Africa (Berg & Wiebes 1992). Although the contemporary geographic ranges of *F. cordata* and *F. ilicina* largely overlap, the former species extends a little farther south and eastward in South Africa.

The habitat selection analysis (Figure 2) discriminated biome affiliations between these species, showing *F. ilicina* to be largely associated with the Nama Karoo in its South African range. In South Africa, the Succulent Karoo, Fynbos and Grasslands biomes were also included in the distribution of *F. cordata*. Phylogenetic patterns of closely related species of *F. ilicina* (Figure 4) have disjunct ranges in west-central (*F. pseudomangifera*) and eastern (*F. usambarensis*) Africa, and suggests fragmentation contributed to vicariant speciation across these regions (Jürgens 1997). Conversely, the range of *F. cordata* is parapatric with its sister species, *F. salicifolia*, and suggests differentiation occurred across the savanna-Karoo divide (Figure 1). *Ficus salicifolia* is widely distributed through the eastern parts of Africa into the Arabian Peninsula, whereas the two subspecies of *F. cordata* (the nominate subspecies and *F. cordata* subsp. *lecardii*) have strongly disparate distributions with *F. cordata* subsp. *lecardii* restricted to the savanna belt extending from central Africa (southern Sudan and Central African Republic) to Senegal in west Africa (Berg & Wiebes 1992). All these contemporary distributions have most likely been driven by the fluctuating expansion and contraction of the savanna, woodland and forest biomes over the last 150 000 years (Dupont et al. 2000; Salzmann & Hoelzmann 2005). The evidence of differences in the breadth of soil water resource utilisation between *F. cordata* and *F. ilicina* (Figure 3) also suggests unique processes or timescales were associated with the occupancy of the Karoo deserts by the lineages of these two species.

The Nama and Succulent Karoo biomes have distinct phytogeographical characteristics that are each part of different Palaeo-Kingdoms (Cowling et al. 1999). Generally, the geology and soil characteristics of South Africa's biomes underlie environmental factors limiting the distribution of the vegetation (Guo et al. 2017). Soil fertility has been shown to be a regionally important factor in the distribution of savanna, along with effective rainfall and seasonal variability of rainfall (Lehmann et al. 2011). However, soil nutrient states between savanna and grassland biomes are strikingly similar and suggest other factors besides nutrient limitation drove vegetation changes in these regions (Gray & Bond 2015). Changes in soil characteristics have also been shown to be independent of changes to community structure in these regions, where interactions involving precipitation and fire regimes were determinants of changes to the vegetation (Dougill et al. 2010). For instance, Fynbos and Succulent Karoo are fire refuge areas that are distinct from the C_4 grass-rich savanna biome that is prone to annual burning (Linder 2014) and suggests a role for fire in niche evolution of *Ficus*. Additionally, the groundwater availability in rocky terrain of the Karoo ranges from depths of 20 to 100 m (De Vries et al. 2000) and might also be an important factor contributing to *Ficus* occupying the Karoo deserts. Generally, mixed historical processes such as rainfall gradients, fire frequency, seasonal variability and topographic features have produced the biogeographic distributions evident in the contemporary communities. Under changing environmental conditions, local adaptation and niche expansion by *F. cordata* and *F. ilicina* are expected to be slow, with population divergence occurring over long periods (Pyron et al. 2015) and possibly under contrasting mechanisms.

Niche expansion and phenotypic integration

Our findings were consistent with at least two independent niche expansions by *Ficus* from their palaeotropical origins (Cruaud et al. 2012) into arid environments. *Ficus cordata* and *F. ilicina* have occupied similar contemporary geographic ranges in arid biomes. This has resulted in the convergence of obligate lithophyte growth forms (Figure 4) and small syconium size in these distantly related lineages. Therefore, the geographic distribution patterns of these traits largely correspond to contemporary water gradients. However, differences between the heritability of the phenotypic traits and in the phylogenetic signal of SWS and PAW, suggest that the expansion into arid environments depended on phenotypic integration (Pigliucci 2003). Correlations or covariances between syconium size and growth form might be altered by changes in environmental conditions. For example, each trait might respond differently to environmental variation according to discrete spatial and temporal scales (Cornwallis & Uller 2009). The phylogenetic over-dispersion (Figure 4) and low probability of heritability of growth form suggests a labile trait important for habitat specialisation. This result is consistent with previous work that compared traits between hemi-epiphytic and non-hemi-epiphytic fig species and showed that ecophysiological traits exhibit phylogenetic lability (Hao et al. 2011). Over-dispersion of traits implies that closely related species may have differentiated between environmental niches (Cavender-Bares et al. 2009). It is possible that the niche expansions by *Ficus* into arid environments occurred along water availability gradients and resulted in selection for habitat specialisation (e.g., Hoffmann & Parsons 1993). Furthermore, given environmental lability in growth form, the relatively strong phylogenetic signal of syconium size suggests a limiting factor on the rate at which *Ficus* is able to adapt to arid conditions.

Syconium size and growth form may each have had a unique role in niche differentiation either locally or across wider regions. Epiphytism in *Ficus* has a role in α-niche (within-community) differentiation as a consequence of variation in ecological requirements and in habitat specificity among species (Nieder et al. 2001). For example, the negative relationship between syconium size and elevation suggested local niche partitioning in tropical habitats occurred at local scales of less than

3 km (Lasky et al. 2014). The ability to cope with water stress and low nutrient availability has been put forward as a key feature underlying the community composition of epiphytes in general (Zotz & Hietz 2001). The convergence of the lithophyte forms in arid habitats, and divergence between *F. ilicina* and *F. cordata* and the lithophytes *F. abutilifolia*, *F. salicifolia* and *F. tettensis* in savanna habitats, suggests a role for growth form in facilitating β-niche (between-community) differentiation. For example, among-population variation in several traits of *Ficus*, including syconium morphology, has been shown to correlate with latitude and precipitation variation (Piedra-Malagón et al. 2011). Both *F. cordata* and *F. ilicina* have a relatively small syconium size (0.5–1.0 cm and 1.5–2.0 cm diameter respectively), but not exclusively so, as the sister species *F. salicifolia*, which is associated with mesic environments, has similar fig size to the nominate subspecies (Berg & Wiebes 1992). Habitat aridity has been shown to be significantly correlated with tree height but not with fig size (Compton & Hawkins 1992).

The associated wasp fauna species richness is comparatively dramatically reduced in these two arid-adapted species with only four (*F. cordata*) and five (*F. ilicina*) fig wasp species developing within each of the host species (Compton & Hawkins 1992), although *F. salicifolia* supports a richness similar to these. Small fig size in combination with a smaller crop size also has implications for wasp population density, with wasp abundance per fig crop dramatically reduced compared to fig species developing in mesic environments. This may have reproductive implications that reduce the efficacy of pollinator dispersal and hence successful location of other fig crops suitable for pollination and oviposition. The arid-adapted lineages may be increasing the prevalence of apomixis, but any evidence for this is scarce (Firetti 2017). Given the negative implications of arid habitats on successful pollination, reproduction by vegetative means may be more advantageous than sexual reproduction for arid-adapted plants, reducing the genetic load associated with small fig and crop sizes, and also reduced wasp population abundance. Overall, one trait may have limited (e.g. the rate) while the other facilitated (e.g. a niche expansion) niche evolution by *Ficus* into arid habitats, as lineages accommodated climate shifts to drier conditions.

Destabilisation of the mutualism

Evidence that supports niche expansions by figs into arid habitats over long periods, suggests that pollinators had ample time to adapt to the changing conditions (i.e., phenotypic matching; Anderson & Johnson 2008). Additionally, niche expansions may have had consequences for populations experiencing marginal habitat quality at their range limits (Bridle & Vines 2007). Demographic processes at the range limits potentially led to changes in the habitat preferences and ecological niche of pollinating wasps. For instance, polyphyletic affiliations of the pollinator genera *Elisabethiella* and *Nigeriella* (Figure 4) did not agree with a co-diversification hypothesis (McLeish & Van Noort 2012). Host shift patterns are consistent with changes to mutualist partners of ancestor lineages of *F. ilicina* and other *Ficus* species in this clade (subsection *Chlamydodorae*). One explanation put forward to explain the relatively high incidence of pollinator host shifts in African *Ficus* is the bias many species exhibit towards smaller syconium sizes (Berg & Wiebes 1992; Renoult et al. 2009). However, it is difficult to connect large-scale geographic changes and adaptive responses with phylogenetic patterns (Ackerly 2003) such as these. The relationship between small syconia and host shifts was not always consistent with the phylogenetic patterns. The role geographic distributions of phenotypes have on host shifts and the diversification of mutualisms is unclear as multiple traits influence partner associations.

Theoretically, partner associations of mutualisms are destabilised by limitations to seed and pollen dispersal (Amarasekare 2004), phenological mismatches (Gilman et al. 2011), and changes to interspecific interactions (Aung et al. 2022). *Ficus* species exhibit mixed densities across their range, which are dependent on seasonality and reproductive constraints on the maintenance of viable populations (Zhang et al. 2014). During environmental change, the fitness of fig and wasp pollinators at the range limits may therefore be determined by physiological tolerance thresholds that differ among respective populations. Dispersal that is dependent on physiological or behavioural phenotypic traits may cause individuals to settle in the environmental conditions that best accommodate their own phenotype and create non-random gene flows and spatial heterogeneity among phenotypes (Jacob et al. 2015). For example, connectivity among patches of the Sonoran Desert fig *F. petiolaris*, and the frequency of foundress visitation, decreased at the range limits (Duthie & Nason 2016). Small population sizes at the limit may be subject to the stochastic sampling of phenotypic variation that causes changes to phenotype means and variances of populations, and with it, enhance drift and destabilise species associations (Bolnick et al. 2011). For instance, geographic disassociations between fig and wasp populations may result in pollinator-effectiveness trade-offs (e.g., Armbruster 2017), which occur when plant fitness is either positively or negatively correlated between co-occurring pollinators. Adaptation in changing environments may have resulted in performance trade-offs among reproductive, physiological or other life-history traits of figs or wasps. If environmental lability in growth form was adaptive, it might strongly influence the evolution of reproductive traits and have feedbacks into the ecology of the mutualism. Any trade-off between ecological and evolutionary factors experienced by either fig or pollinator, might have also coincided with changes in mutualistic partners.

Conclusion

The niche expansions by *F. ilicina* and *F. cordata* involved distinct historical processes occurring over long periods and possibly under contrasting mechanisms. Niche expansions by *Ficus* into arid environments occurred along water availability gradients and resulted in selection for habitat specialisation. The environmental lability evident in growth form and the relatively strong phylogenetic signal of syconium size may have limited the rate at which *Ficus* was able to adapt to arid conditions. The selection for traits that limited the rate of niche expansions potentially destabilised mutualist partnerships and promoted host shifts.

Acknowledgements

This project was made possible with the assistance of the Claude Leon Foundation. We would like to thank the South African National Biodiversity Institute (SANBI) for providing part of the sample data used in this paper. We would also like to thank Prof. Roland E. Schulze, who provided the data from his 'South African atlas of climatology and agrohydrology', and we thank Leslie Powrie and Mike Rutherford for providing the biome data from their project on The Vegetation of South Africa, Lesotho and Swaziland. This paper is partially supported financially by the National Research Foundation, Ref. no. IFR2009090800013. This work was in part supported by grant BFU2015-60418-R, Plan Estatal de I+D+I, Spain. We are grateful for the assistance of Marius Masencamp and his tireless field expedition support.

Competing interests

The authors declare that they have no financial or personal relationship(s) that may have inappropriately influenced them in writing this article.

Authors' contributions

M.J.M and D.G. conducted the data analysis and M.J.M. prepared the first draft of the paper. S.v.N., D.G. and M.J.M. reviewed and edited the paper for final publication. All authors contributed to the development of the study.

Ethical considerations

This article followed all ethical standards for research without direct contact with human or animal subjects.

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Supplementary material

S1. Calculation of soil water variables

Climate variables and parameters interact and combine with each other and with the soil to generate the environment which the plant grows in, and water becomes available to the plant through soil moisture (Schulze et al. 2007). The variables, days of year with severe soil water stress (SWS) and plant available water (PAW), are used to test whether there is a relationship with syconium size. Days of year with severe soil water stress (SWS) indicates the number of days per year at which soil water content would be at critical plant stress. Severe soil water stress refers to the soil water content at which total evaporation is reduced to below 20% of the maximum evaporation: $\theta < 0.2\ E/E_m$. With θ as the actual soil water content, E is the total evaporation of a plant/soil system and E_m is the maximum evaporation that could take place. Plant available water (PAW) is the water in the soil profile that is readily available to plants. In this case PAW = θ_{DUL} - θ_{PWP}. With PAW as the plant available water, θ_{DUL} as the drained upper limit of soil water, and θ_{PWP} as the permanent wilting point of soil water. The plant available water indicates the storage of water available, and therefore it depends on the soil texture and the soil profile depth and the geological formations (Schulze 2007). The centre-west parts of South Africa have low plant available water and mostly at less than 40 mm deep (Schulze & Horan 2007).

S2. MCMCglmms

Growth form was treated as a multinomial variable with J – 1 linear predictors with J categories (Hadfield 2010). The priors passed to the Markov chain Monte Carlo generalised linear mixed model (MCMCglmm) take three parts that specify the *R*-structure, *G*-structure, and fixed effects (Hadfield 2010). The term *G* is used to describe a covariance matrix of the random effects, and *R* as the covariance matrix of the residual variances that are assumed to follow an inverse-Wishart distribution. The *R*- and *G*-structures use the scalar parameters *V* and *nu* to describe the inverse-Wishart distribution. A third parameter, *fix*, can be specified (i.e. a *fixed* variance component is not estimated) so that the model is free to estimate the other variance components. To test and compare the phylogenetic dependencies of each phenotype, we fixed priors for the *R*- and *G*-structure (as either 0.95 or 0.05 of phenotype variance) using an intercept model (with no fixed factors). By conditioning the variance structure of the model in this way to favour either the phylogeny or the residual component, we compared the respective contributions of each component to phenotypic variation. The deviance information criterion (DIC) was used to compare model fit. The DIC is conceptually similar to the Akaike Information Criterion, with lower values indicating better model fit (Spiegelhalter et al. 2002). The Markov chains of the intercept models were run for 5.0×10^6 iterations with a burnin of 10 000 and a thinning interval of 1 000.

Supplementary Table S1

Ficus species used in the canonical outlying mean index (OMI) analyses

Taxon	***n***	**OMI code**
Ficus abutilifolia	91	1
Ficus bizanae	15	2
Ficus bubu	5	3
Ficus burkei	56	4
Ficus burtt-davyi	51	5
Ficus cordata	10	6
Ficus cordata subsp. *cordata*	61	7
Ficus craterostoma	102	8
Ficus glumosa	83	9
Ficus ilicina	17	10
Ficus ingens	117	11
Ficus lingua	4	12
Ficus lutea	22	13
Ficus natalensis	40	14
Ficus natalensis subsp. *graniticola*	20	15
Ficus petersii	13	16
Ficus polita	5	17
Ficus polita subsp. *polita*	7	18
Ficus salicifolia	72	19
Ficus sansibarica	7	20
Ficus sansibarica subsp. *sansibarica*	16	21
Ficus stuhlmannii	31	22
Ficus sur	131	23
Ficus sycomorus	20	24
Ficus sycomorus subsp. *gnaphalocarpa*	1	25
Ficus sycomorus subsp. *sycomorus*	41	26
Ficus tettensis	21	27
Ficus thonningii	123	28
Ficus tremula	3	29
Ficus tremula subsp. *tremula*	4	30
Ficus trichopoda	18	31

Supplementary Table S2

Growth form categories used to model *Ficus* species in the MCMCglmm analyses; 1 = lithophyte, 2 = tree, 3 = hemi-epiphyte, 4 = lithophyte–hemi-epiphyte, 5 = hemi-epiphyte–tree, 6 = lithophyte–tree, 7 = all forms

	Lithophyte	**Hemi-epiphyte**	**Tree**	**Code**
F. abutilifolia	1	-	-	1
F. bizanae	1	2	-	4
F. bubu	1	2	3	7
F. burkei	1	2	3	7
F. burtt-davyi	1	2	3	7
F. cordata	1	-	-	1
F. cordata subsp. *cordata*	1	-	-	1
F. craterostoma	1	2	-	4
F. glumosa	1	-	3	6
F. ilicina	1	-	-	1
F. ingens	1	-	3	6
F. lingua	-	2	-	3
F. lutea	-	2	3	5
F. natalensis	1	2	3	7
F. natalensis subsp. *natalensis*	1	2	3	7
F. petersii	-	2	3	5
F. polita	1	2	3	7
F. polita subsp. *polita*	1	2	3	7
F. salicifolia	1	-	3	1
F. sansibarica	-	2	-	3
F. sansibarica subsp. *sansibarica*	-	2	-	3
F. stuhlmannii	-	2	3	5
F. sur	-	-	3	2
F. sycomorus	-	-	3	2
F. sycomorus subsp. *gnaphalocarpa*	-	-	3	2
F. sycomorus subsp. *sycomorus*	-	-	3	2
F. tettensis	1	-	-	1
F. tremula	-	2	3	5
F. tremula subsp. *tremula*	-	2	3	5
F. thonningii	-	2	3	5
F. trichopoda	-	-	3	2

Supplementary Table S3

The posterior distributions of MCMCglmm coefficients of mean syconium size and growth form responses explained by within- and between-species variance. CI = 95% credible interval. The term *G* describes a covariance matrix of the random effects and *R* as the covariance matrix of the residual variances. The Bayesian *p*-value (*pMCMC*) is (2×) the proportion of values from the posterior estimate that are of the opposite sign to the parameter calculated from the Monte Carlo sampling and provides a way to assess variable support.t

	Variable	**Posterior mean**	**Lower CI**	**Upper CI**	**Effective sample**	***pMCMC***
Syconium size						
G-structure	Phylogeny	1.040	0.335	1.962	1146	**-**
	Taxon	0.015	0.000	0.059	990	**-**
R-structure	Residual	0.030	0.020	0.039	990	**-**
	Species mean PAW	-1.051	-1.758	-0.237	844	**0.008**
	Within-species PAW	0.002	-0.136	0.135	1106	0.980
	Species mean SWS	-0.834	-1.607	-0.072	990	**0.046**
	Within-species SWS	-0.005	-0.235	0.250	990	0.962
Growth form						
G-structure	Phylogeny	1.025	0.941	1.116	2095	-
	Taxon	1.036	0.946	1.134	1980	-
R-structure	Residual	200	200	200	0*	-
	Species mean PAW	273.9	219.5	324.8	319	**<0.001**
	Within-species PAW	0.000	-4.071	4.154	1980	0.991
	Species mean SWS	-233.6	-276.0	-192.0	317	**<0.001**
	Within-species SWS	0.047	-7.830	7.370	1980	0.996

*Fixed prior for categorical response

Supplementary Table S4

Intercept models showing the 95% highest posterior density intervals of the distribution of the variance for mean syconium size and growth form responses. The term *G* describes a covariance matrix of the random effects, and *R* as the covariance matrix of the residual variances. The table shows models with different prior R- and G-structure variance prior assumptions (as either 0.95 or 0.05 of phenotype variance respectively). CI = Credible Interval; DIC = Deviance Information Criterion

Variance component	**Variance prior**	**Factor**	**Posterior mean**	**Lower CI**	**Upper CI**	**Effective sample**	**DIC**
Syconium size							
G-structure	0.05	Tree	252.40	120.40	394.90	990	-739.24
		Taxon	0.83	0.21	1.76	990	
R-structure	0.95	Null	0.08	0.08	0.09	990	
G-structure	0.95	Tree	240.40	87.37	424.70	990	-4292.76
		Taxon	11.48	3.85	21.44	990	
R-structure	0.05	Null	0.00	0.00	0.00	990	
Growth form							
G-structure	0.05	Tree	2.85	0.00	6.63	590	3090.20
		Taxon	8.54	4.57	13.22	568	
R-structure	0.95	Null	4.70	4.70	4.70	*0	
G-structure	0.95	Tree	55.85	16.01	90.13	19	3365.89
		Taxon	13.24	0.57	30.02	14	
R-structure	0.05	Null	0.25	0.25	0.25	*0	

*Fixed variance prior for categorical response.

Supplementary Table S5

The posterior distribution of the MCMCglmm coefficients for growth form and mean syconium size responses as explained by geobiological variables (biome, aspect, slope), PAW (plant available water), SWS (soil water stress), and phylogeny. CI = 95% credible interval. A relatively high effective sample indicates that the model is mixing well. Strong effects indicated with bold *pMCMC* value. The term *G* describes a covariance matrix of the random effects, and *R* as the covariance matrix of the residual variances

	Variable	**Posterior mean**	**Lower CI**	**Upper CI**	**Effective sample**	***pMCMC***	**DIC**
Syconium size							
G-structure	Phylogeny	2.088	0.931	3.546	990		9117.48
	Taxon	0.008	0.000	0.026	990		
	Biome	0.006	0.000	0.021	990		
	Aspect	0.002	0.000	0.005	990		
R-structure	Residual	0.030	0.020	0.039	961.6		
Fixed effects	PAW	-0.033	-0.159	0.109	990	0.620	
	SWS	-0.072	-0.339	0.187	990	0.606	
	Elevation	0.002	-0.126	0.154	990	0.976	
	Slope	-0.048	-0.215	0.155	990	0.616	
Growth form							
G-structure	Phylogeny	1.083	0.989	1.183	990		735.88
	Taxon	1.144	1.049	1.261	990		
	Biome	1.011	0.920	1.090	896.1		
	Aspect	1.000	0.916	1.095	990		
R-structure	Residual	200	200	200	0		
Fixed effects	PAW	2.540	0.517	4.575	818.5	**0.014**	
	SWS	-13.174	-15.772	-10.532	1127.8	**< 0.001**	
	Elevation	-2.288	-4.217	-0.089	1087.3	**0.040**	
	Slope	2.587	0.309	4.884	990	**0.034**	

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SANBI
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BOTHALIA – African Biodiversity & Conservation
ISSN: (Online) 2311-9284, (Print) 0006-8241

Notes on morphological characteristics and life history strategy of the genus *Acanthopsis* Harv. (Acanthaceae)

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Dates
Submitted: 28 April 2023
Accepted: 19 January 2024
Published: 21 May 2024

How to cite this article:
Steyn, H.M. & Van Wyk, A.E., 2024, ‘Notes on morphological characteristics and life history of the genus *Acanthopsis* Harv. (Acanthaceae)’, *Bothalia* 54, a7. http://dx.doi.org/10.38201/btha.abc.v54.7

Background: Morphological characteristics and life history strategies are vital in the success of plants to inhabit specific areas. Until recently the genus *Acanthopsis* was taxonomically poorly understood, and a recent revision rectified this aspect. The group comprises 20 species, all confined to arid parts of South Africa and Namibia. Much regarding the life history and ecology of the genus was still unknown.

Objectives: Members of the genus *Acanthopsis* adapted to harsh environmental conditions have evolved an array of functional traits to enhance their chances of survival. The present contribution focuses on a select few of these traits, with discussion centred around them.

Methods: This paper gives an overview of some casual and anecdotal observations made on the morphological characteristics and life history strategy during the taxonomic study.

Results: Significant adaptations include a perennial subshrub habit, spinous inflorescences/infructescences, and flowers exhibiting the classical syndrome for insect pollination, likely by insects possessing elongated proboscises. Additionally, the seeds are myxospermous and undergo dispersal solely when there is an ample supply of water for germination. Noteworthy is the prompt germination of seeds, occurring within 24 h.

Conclusion: Certain observations may potentially serve as catalysts for further, more in-depth investigations into the ecological significance of specific morphological traits and how the species might respond to anticipated future changes in temperature and precipitation.

Keywords: habit, functional traits, inflorescences, life form, morphology, myxospermy, pollen, pollination, seed dispersal.

Introduction

The success of plants to inhabit specific areas lies in the combination of plant functional traits, life history strategy and the success of dealing with competition, disturbance and environmental stress. The life history strategy of a plant can be defined as the patterns and timing of events (related to survival and reproduction) in a plant’s life, including germination, flowering, fruiting and dispersal. According to Adler et al. (2014) there are strong relationships between plant functional traits (e.g., life form, plant height, leaf size and seed dispersal mode) and plant life histories. The life form classification of Raunkiaer (1934) is probably one of the best known classification systems for categorising plants and is based on the position of the plant’s renewal (perennating) buds during seasons with adverse conditions. Plants have evolved three major strategies depending on the degree of disturbance and stress, and can be labelled as competitors, stress-tolerators or ruderals (Grime 1977).

Acanthopsis Harv. (Acanthaceae) is a distinct and easily recognisable genus closely related to the genus *Blepharis* Juss. Both genera can be described as stress-tolerant plants (growing in habitats with high environmental stress and low disturbance) (Grime 1977; Bornhofen et al. 2011). The genus *Acanthopsis* is endemic to southern Africa (Namibia, Northern & Western Cape, South Africa) and most species are found in exposed habitats in full sun in rocky, sandy soils in areas that receive less than 200 mm of rainfall per year. The Succulent Karoo Biome is particularly rich in *Acanthopsis* diversity, with 21 of the 23 taxa occurring here. This biome is associated with the presence of low winter rainfall and extreme summer aridity (along the coast and west-facing Great Escarpment, the rainfall is supplemented by coastal fog) (Steyn et al. 2019).

The biogeography and conservation status of members of *Acanthopsis*, as well as the taxonomic importance of the indumentum, were dealt with by Steyn et al. (2019) and Steyn and Van Wyk (2021) respectively. The aim of this paper is to give an overview of some noteworthy, albeit often casual or anecdotal, observations made on the morphological characteristics and life history strategy during the taxonomic study that may help explain the biology of the genus in relation to the prevailing habitat conditions. Additionally, it is anticipated that certain observations may serve as catalysts for subsequent, more in-depth investigations into the ecological significance of specific morphological traits.

Research materials and methods

Materials

Taxonomic decisions were based on a detailed comparative morphological study of ± 400 herbarium specimens from various herbaria worldwide. This study was conducted at the National Herbarium (PRE) of the South African National Biodiversity Institute (SANBI), South Africa. Relevant herbarium specimens held at BOL, K, KMG, M, NBG, NMB, P, PRE, PRU, SAM (in NBG), WIND and Z together with high resolution images of herbarium specimens on JSTOR (2018) and from the herbaria of B-W, BM, GZU, S and TCD were studied (abbreviations of herbaria follow Holmgren et al. 1990; Thiers 2023).

Fieldwork was done over a period of three growing seasons to assess the variation of live plants in nature, and to collect spirit material, herbarium specimens, DNA samples and photographic images.

Methods

All measurements were taken from herbarium specimens, or in the case of floral parts, mostly from additional pressed material collected by the authors. Leaf and floral samples were taken from herbarium specimens and studied under a stereomicroscope (Zeiss Discovery V8) or light microscope (Zeiss Axio). For scanning electron microscope (SEM) work, a high resolution field emission SEM (Zeiss) housed in the Laboratory for Microscopy and Microanalysis, University of Pretoria and a desktop SEM (Phenom Pure+), in the National Herbarium, SANBI, were used. Digital images to illustrate the general morphology were obtained with a Zeiss Discovery V8 stereomicroscope and a Zeiss Axio light microscope.

Terminology follows Beentje (2016). Descriptors used to indicate abundance and frequency follow Schmid (1982).

Permitting

Relevant collecting permits were obtained before the collection of herbarium specimens.

Results

Life form and habit

The genus *Acanthopsis* comprises different life forms according to the classification of Raunkiaer (1934). Most of the species are considered chamaephytes, with *A. disperma* Nees and the annual form of *A. hoffmannseggiana* (Nees) C.B.Clarke as therophytes. The perennial rosette form of *A. hoffmannseggiana* may be classified as a hemicryptophyte.

Within *Acanthopsis*, the shrublet (dwarf shrub) group is one of the most readily recognisable entities in a genus otherwise characterised by acaulescent herbs or compact subshrubs. There is a gradual increase in woodiness, branching and internode length from annual/perennial herbs to subshrubs and shrublets. The shrublet group can be distinguished in usually being virgate, up to 25–40(–60) cm tall, with well-developed branches and clearly visible internodes; the latter are usually up to 10–20(–25) mm long. Shrublet species usually have scattered leaves (well-spaced) along woody stems (Figure 1C & D). The shrublet group includes the following species: *A. dregeana* H.M.Steyn, *A. erosa* H.M.Steyn, *A. horrida* (Nees) Nees and *A. spathularis* (Nees) Schinz.

Subshrubs are much more compact plants, up to 25(–30) cm tall, with gnarled stems and reduced (usually not visible) internodes, usually < 5(–8) mm long, with

Figure 1. Different habits found in *Acanthopsis*. A, acaulescent herb; B, compact subshrub; C, shrublet (cushion-shaped); D, shrublet (virgate). Photographs: A, B, the authors; C, D: M. Koekemoer.

fascicled leaves (Figure 1B). Compact subshrubs are the most common in the genus and include *A. adamanticola* H.M.Steyn, *A. carduifolia* (L.f.) Schinz, *A. dispermoides* H.M.Steyn, *A. glabra* (Nees) H.M.Steyn, *A. glandulopalmata* H.M.Steyn, *A. glauca* (E.Mey. ex Nees) Schinz, *A. hoffmannseggiana*, *A. insueta* H.M.Steyn, *A. ludoviciana* H.M.Steyn, *A. nitida* H.M.Steyn, *A. pagodiformis* H.M.Steyn, *A. scullyi* (S.Moore) Oberm., *A. tetragona* H.M.Steyn, *A. tuba* H.M.Steyn and *A. villosa* H.M.Steyn.

Acaulescent/rosulate herbs, with leaves in a basal rosette, are almost restricted to the annual or short-lived perennial species of *A. disperma* and *A. hoffmannseggiana*, while young plants of *A. dispermoides*, *A. glabra*, *A. pagodiformis* and *A. scullyi* could appear acaulescent (Figure 1A).

Certain species have pioneer or weedy tendencies, and they thrive under conditions of disturbance and degradation often caused by overgrazing (e.g., *Acanthopsis carduifolia*, *A. disperma*, *A. hoffmannseggiana* and *A. scullyi*). However, these species have never been observed to become invasive.

Inflorescences, flowers and flowering time

All species of *Acanthopsis* have bracteate spikes (Figure 2), which are solitary (terminal) in subshrub and shrublet species or in clumps at the base of the leaves in the rosulate species. The spikes range from lax where the inflorescence axis among the bracts is nearly always exposed with successive bract laminas only slightly overlapping, to dense, where the inflorescence axis among bracts is never exposed with the bract laminas deeply overlapping. The floral bracts are stiff, apically 3–7-lobed, with each lobe ending in a simple or compound spine.

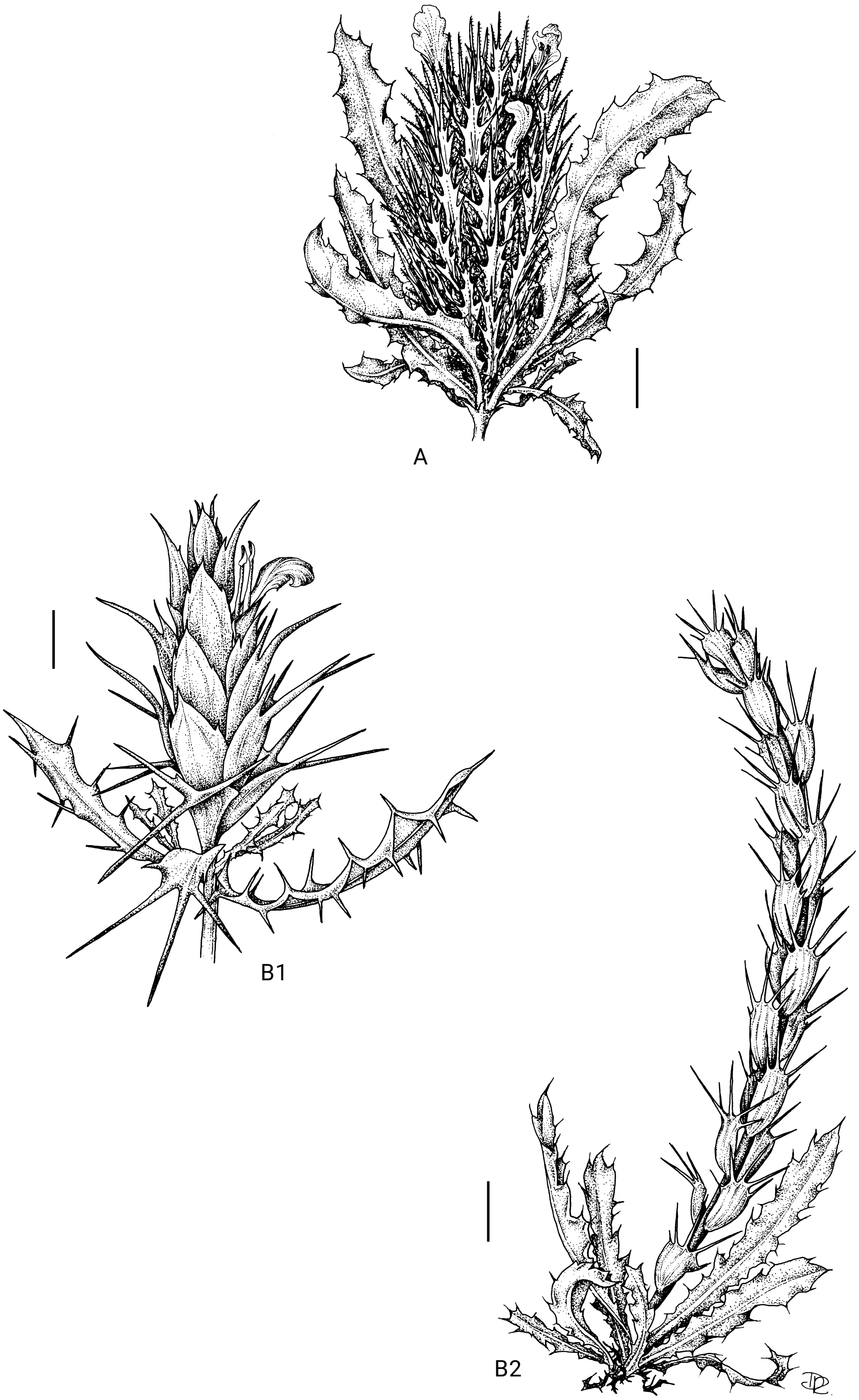

Figure 2. Types of inflorescences found in *Acanthopsis* based on the density of individual flowers and their bracts. A, dense (> 60% bract overlap); B, lax (B1, 30–60% bract overlap; B2, < 30% bract overlap). Scale bar: 10 mm. Artist: Daleen Roodt.

The flowers consist of a 4-partite calyx and tubular corolla. The corolla of *Acanthopsis* is zygomorphic, 1-lipped and 5-lobed, with the outer lobes much reduced (except in *A. tuba*) and the lip much longer than the tube (except in *A. tuba*) (Figure 3). The corollas of *Acanthopsis* have ascending cochlear aestivation (abaxial corolla lobe is always wholly overlapping the lateral lobes) (Scotland et al. 1994). The corolla sizes generally vary between 23–25 × 9–11 mm, with the longest corollas found in *A. glandulopalmata*, *A. scullyi*, *A. tetragona* subsp. *pedunculata* and *A. tuba*. *Acanthopsis tuba* has the longest flowers in the genus (45–50 mm long), which is probably an adaptation to a specific pollinator. Corollas are usually lilac to purple with darker veins (e.g., *A. disperma*, *A. horrida* and *A. dregeana*) or whitish/cream with purple veins (annual form of *A. hoffmannseggiana* as well as *A. scullyi*). The corolla throat varies from white or cream to lemon-yellow (Figure 4). The reduced outer corolla lobes are usually the same colour as the corolla throat, except for *A. horrida*, *A. tuba* and *A. villosa*, where the outer lobes are the same colour as the corolla limb, namely lilac to purple.

Figure 3. Corolla, androecium and gynoecium of *Acanthopsis* flowers. A, corolla, *A. tuba* (*Von Staden 9139*); B, corolla, *A. horrida* (*Koekemoer 4370*, PRE); C, androecium, *A. horrida* (*Koekemoer 4370*, PRE); D, gynoecium and one lateral sepal of calyx; note the tuft of glandular hairs at base of style, *A. scullyi* (*Steyn 1911*, PRE). Scale bar: A, B = 10 mm, C, D = 1 mm. Artist: Daleen Roodt.

Figure 4. Corolla of *Acanthopsis* flowers showing colour variation. A, *A. glauca*; B, *A. horrida*; C, *A. hoffmannseggiana*; D, *A. scullyi*. Photographs: A, B, M. Koekemoer; C, D, the authors.

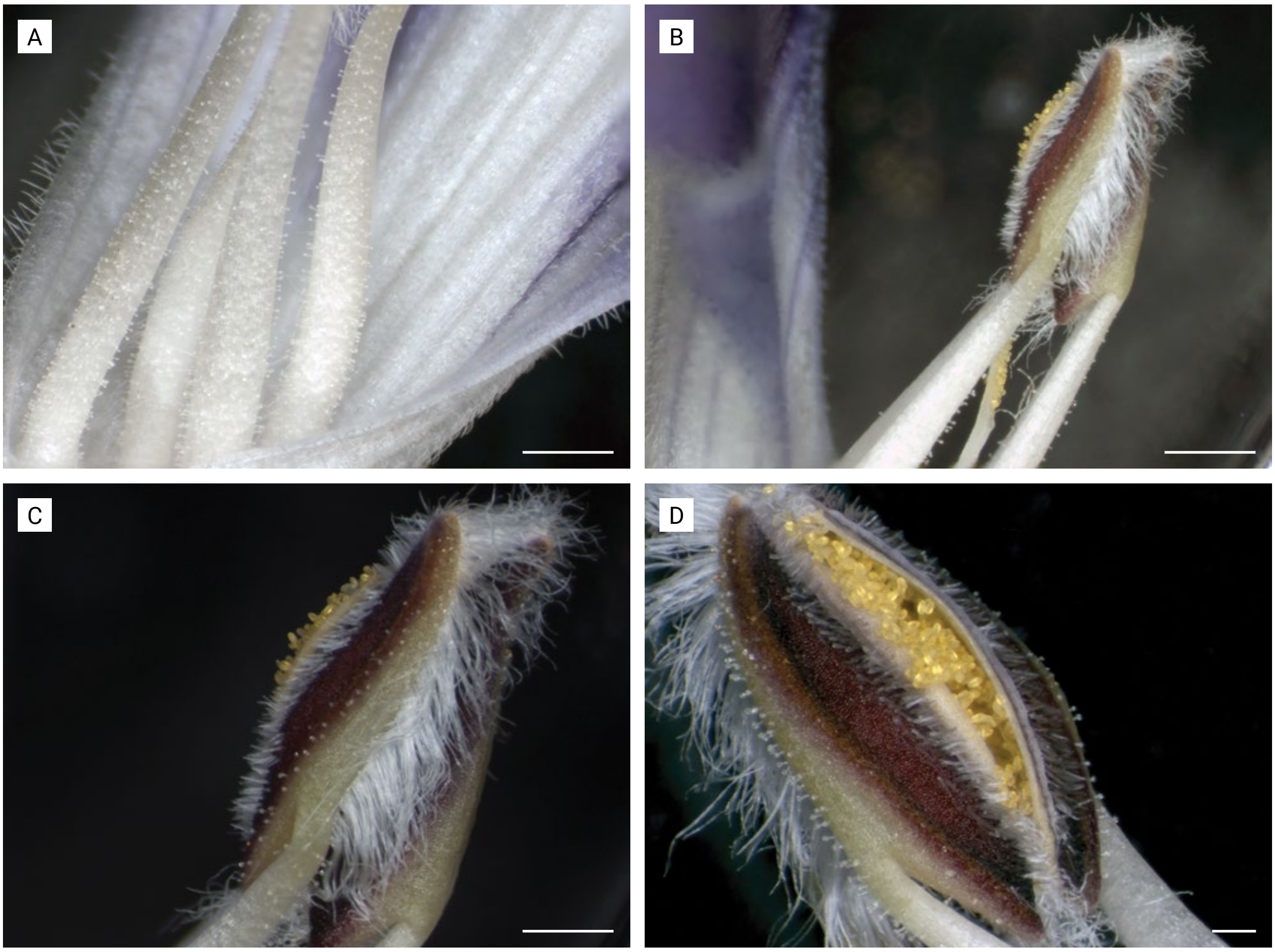

Figure 5. Androecium of *Acanthopsis disperma* flowers. A, stout filaments; B, anthers and style; C and D, anthers, showing long hairs and pollen grains exposed on the side facing the corolla lip. Scale bar: A = 0.8 mm, B = 0.7 mm, C = 0.5 mm, D = 0.2 mm.

The androecium comprises four fertile stamens of equal length and shape, without staminodes. The filaments are stout and the anthers densely bearded along the lateral edge (Figures 3 & 5), connivent (held together by hairs), monothecal, sub-basifixed and non-versatile. In *Acanthopsis* the filaments are without an appendage at the tip – this is present in *Blepharis*. The anthers are introrse, but expose the bright yellow pollen through an opening between the two anterior anthers on the side facing the corolla lip (Figure 5). In *Acanthopsis* the style is filiform with an unlobed stigma (one lobe is highly reduced). In *Blepharis* there are two elliptic or rounded patches of very short glandular hairs on the same side at the base of the style, while in *Acanthopsis*, the base of the style is covered with a ring or a patch of glandular hairs (Figure 3D). The taxonomic and functional significance of these glandular hairs, as well as the hairs on the anthers, needs further investigation.

Most species flower during spring and early summer with the exception of *A. disperma* and *A. hoffmannseggiana*, which often flower during autumn. The difference in flowering time is probably the result of late summer rain in the transition areas between summer and winter rainfall where these species are found.

Pollen and pollination

Acanthaceae, a classical eurypalynous family, is noted for its wide variety of pollen types. This fact was first highlighted by Radlkofer (1883), and the variation in the morphology of pollen grains is of considerable diagnostic value (e.g., Lindau 1893, 1895; Bremekamp 1944, 1965; Raj 1961; Munday 1980; Immelman 1987; Balkwill & Getliffe Norris 1988; Graham 1988; Furness 1990, 1991, 1995, 1996; Scotland & Vollesen 2000; Perveen & Qaiser 2010; House & Balkwill 2016). Most species of *Acanthopsis* have beige to orange-brown anthers with the exception of *A. adamanticola*, *A. disperma*, *A. erosa*, *A. hoffmannseggiana*, *A. horrida*, *A. spathularis* and *A. tuba*, which have dark brown to purple-black anthers. In *Acanthopsis* pollen is shed as monads. Grains are isopolar, prolate to perprolate (Polar axis/Equatorial diameter = 1.45–2.17), 3-colpate, with a triangular outline in polar view and an elliptical outline (somewhat angular in *A. tuba*) in equatorial view (Figure 6). The exine sculpturing of the mesocolpi is essentially microreticulate to foveolate with some variation adjacent to colpi (Figure 6). A distinct elevated ridge surrounds colpi with the surface adjacent to the ridge, usually verrucate (rugulate in *A. tuba*).

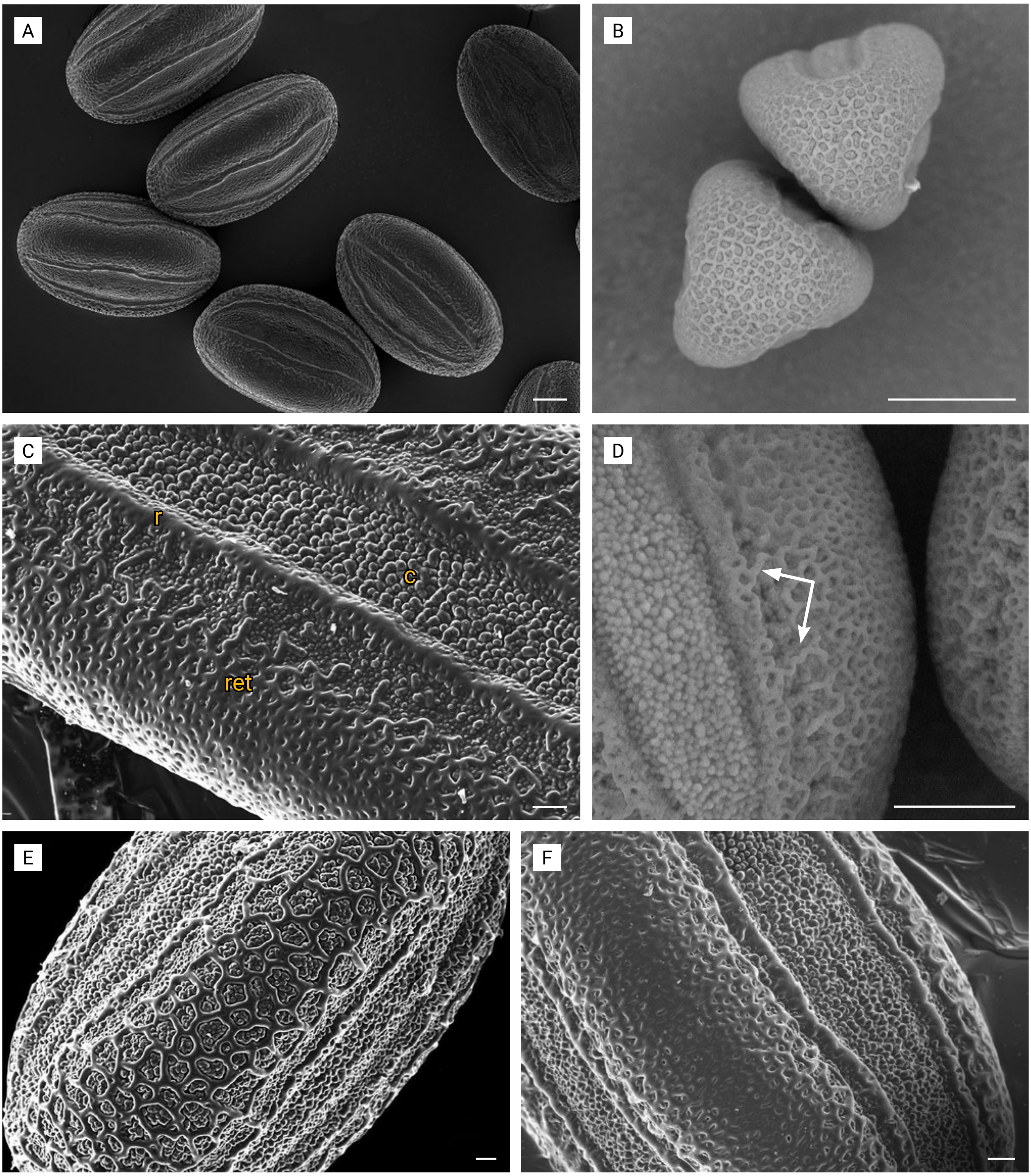

Figure 6. SEM images of pollen grains (unacetolised) of *Acanthopsis*. A, *A. glauca*, equatorial view (*Steyn 1888*, PRE); B, *A. hoffmannseggiana* typical form, polar view (*Steyn 1900*, PRE); C, *A. spathularis*, showing reticulum (ret), colpus (c) and ridge (r) (*Steyn 2135*, PRE); D, *A. adamanticola*, showing muri (see arrows) connecting the ridge and reticulum (*Smook 11204*, PRE); E, *A. carduifolia*, surface sculpturing of mesocolpium reticulate (*Koekemoer 4260*, PRE); F, *A. tetragona* subsp. *tetragona*, surface sculpturing of mesocolpium microreticulate to foveolate (*Steyn 1848*, PRE). Scale bar: A = 10 μm, B = 20 μm, C = 2 μm, D = 8 μm, E, F = 2 μm.

Muri connecting the ridge with the reticulum can be absent or present (Figure 6).

Furness (1996) studied pollen of the so-called 'group with long-exserted stamens and bone-like filaments' within Acantheae, which includes *Acanthopsis*, *Acanthus*, *Blepharis* and *Sclerochiton*. She stated that pollen morphology was taxonomically significant at genus, as well as species level, and five pollen types, with ten subtypes, were described (Furness 1996). Four species of *Acanthopsis* were included in the above-mentioned study, and it was concluded that pollen of *Acanthopsis* is dissimilar to that found in the other genera, being relatively large compared to the closely related *Acanthus*

Figure 7. The flowers of *A. horrida* showing the stigma deflected towards the corolla lip. Photograph: M. Koekemoer.

and *Blepharis*. Furness (1996) distinguished *Acanthopsis hoffmannseggiana* from *A. carduifolia*, *A. disperma* and *A. spathularis* (misapplied name = *A. horrida*) based on its pollen type. However, during the current study, it was found that the presence/absence of muri joining the ridge of tectum to the reticulum, used by Furness (1996) to distinguish between pollen types, is variable among samples within the above-mentioned species and *A. disperma* and *A. hoffmannseggiana* display both pollen types.

From images taken in the field of plants in flower, it is clear that the style is shortly exserted at the top of the anthers (at a stage without any obvious pollen grains presented by the anthers or the protruding style), and it was suspected that the flowers are protogynous. However, preliminary observations from a cultivated specimen of *A. disperma* indicated that there is no temporal separation of pollen maturation and stigmatic receptivity within a flower. Although the style lengthens until it is exserted from the anther 'tube' and the stigma deflects towards the corolla lip (Figure 7), it does not seem to function as a 'pollen presenter' (Ladd & Donaldson 1993).

Hardly any information is available on the pollinators of *Acanthopsis*, but the dark purple veins on the corolla probably serve as nectar guides to insect pollinators. Flowers of certain species of *Blepharis* are known to be visited and pollinated by bees, wasps and pollen wasps (Gess & Gess 2010, 2014) (Figure 8). The flowers of *Acanthopsis* have no noticeable scent during the day, but nectar was observed in fresh flowers as a droplet at the base of the corolla tube. Fruit flies (Tephritidae) and ants (*Crematogaster* species) were often observed on *Acanthopsis* flowers (before and after anthesis) (Figure 8), and bee flies were observed visiting populations of *A. tuba* plants (P. van Wyk, pers. comm. 2017; F. Grenier, pers. comm. 2018).

Fruit and seed

The fruit in *Acanthopsis* is a bilocular capsule enveloped in a persistent zygomorphic calyx. All members of *Acanthopsis* have ovate, flattened, glabrous, 2-seeded capsules with ovate, flattened seeds covered with long white hygroscopic hairs. As the availability of capsules and seeds was limited (especially in some taxa, e.g., *A. spathularis* and *A. tuba*), the full taxonomic potential of these characters, particularly as a source of diagnostic characters for species, could not be established. However, in general, the capsules are 6–8 × 3–4 mm and the seeds 4 × 3 mm. The capsules of *A. carduifolia*, *A. nitida* and *A. scullyi* tend to be slightly bigger (8–9 × 3–4 mm) than the rest of the taxa. *Acanthopsis tetragona* subsp.

Figure 8. Insects observed on *Acanthopsis* flowers. A, fruit fly on *A. hoffmannseggiana*; B, fruit fly and ant on *A. nitida*; C, long-proboscid bee fly probing a flower of *A. tuba*. Photograph: A, B, the authors; C, F. Grenier.

pedunculata has relatively large seeds (6 × 5 mm) compared to the other taxa [for more information, see Steyn (2018)].

Despite water being a limiting factor in arid areas, hydrochory (here defined as dispersal by rain or dew) plays an important part in this environment (Van Rheede van Oudtshoorn & Van Rooyen 1999). *Acanthopsis* and *Blepharis* are antitelechoric genera where seed dispersal does not take place immediately after the fruit has ripened, but the mature capsules are retained unopened on the plant until the conditions are favourable (sufficient water for germination is present) (Gutterman 1994; Vollesen 2000). In *Acanthopsis* the dry capsule remains covered (protected) by the hydrochastic bract and four sepals, and only upon wetting does the bract diverge (open up) and the upper and lower sepals separate to expose the apex of the capsule (Figure 9). Gutterman et al. (1967) reported that upon wetting, capsules of *Blepharis persica* (Burm.f.) Kuntze [= *B. ciliaris* (L.) B.L.Burtt] explode, and seeds are dispersed dry. The seeds of *Acanthopsis* were very rarely observed to be forcefully expelled from the mature but relatively young capsule (but see next paragraph) upon wetting or even after scarification of the apex, as observed in *Blepharis* by Gutterman et al. (1967). Even when moistened, the apex of the *Acanthopsis* capsule (apical 'lock' according to Gutterman et al. 1967) usually had to be damaged before the capsule opened up slightly, and the seeds were exposed but usually not ejected.

Gutterman et al. (1967) and Van Rheede van Oudtshoorn and Van Rooyen (1999) argued that the rate and degree of separation of the sepals vary with their age, implying that the studied infructescences of *Acanthopsis* were possibly not weathered (old) enough for the capsules to explode and eject the seeds as mentioned above. During an irrigation experiment in autumn 2020, infructescences of different species of *Acanthopsis* collected in 2015 were indeed seen to eject their seeds after wetting (receiving a mist spray for approximately 10 minutes), thus supporting the hypothesis that age of fruit and ejection of seeds are linked.

The hygroscopic hairs covering the seeds of *Acanthopsis* species are mucilaginous. They immediately start

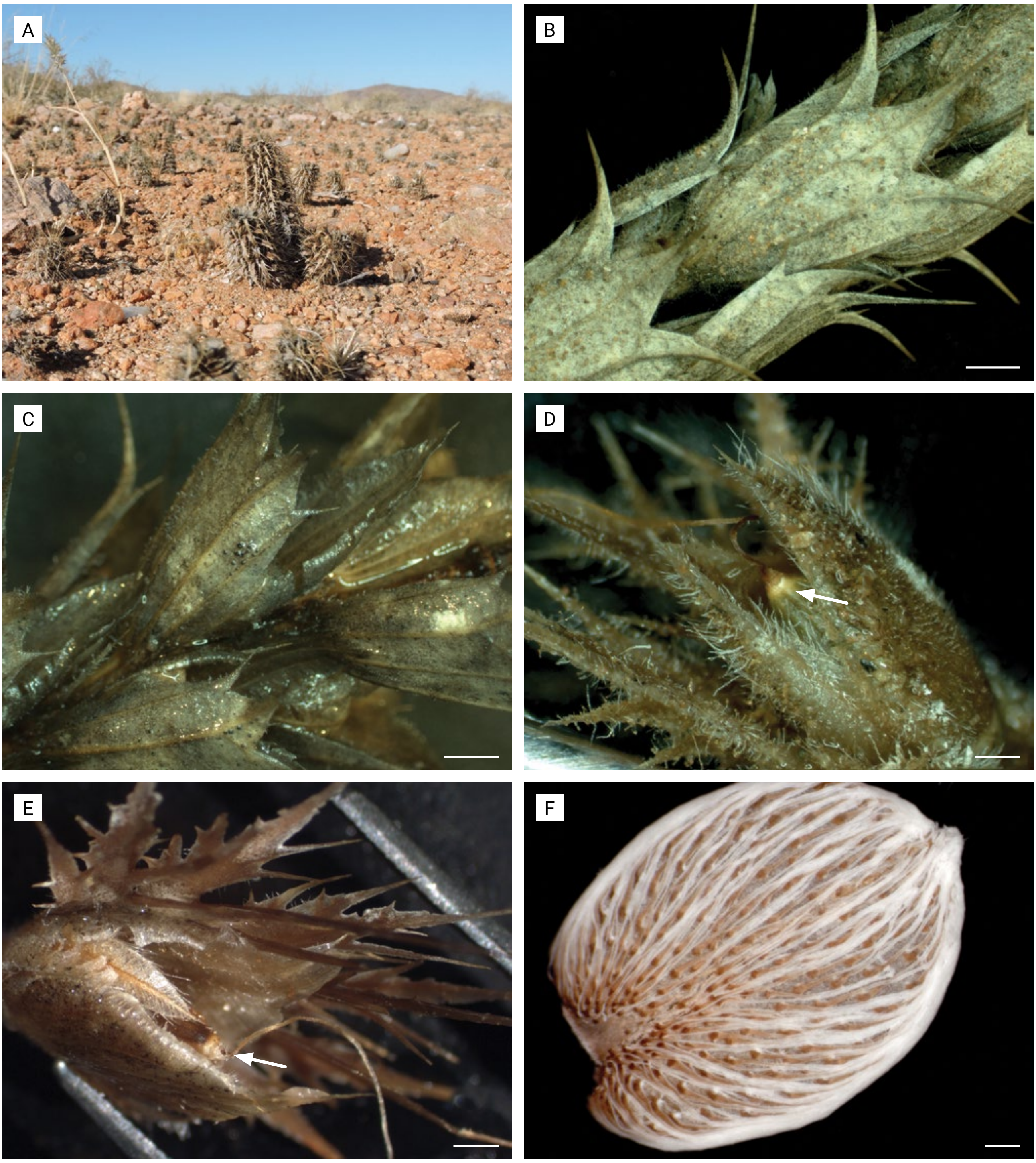

Figure 9. Mature *Acanthopsis* infructescence morphology. A, persistent dry infructescences of *A. hoffmannseggiana* typical form; B, dry infructescence, *A. scullyi* (*Steyn 1911*, PRE); C, wet infructescence, *A. scullyi* (*Steyn 1911*, PRE); D and E, opened sepals exposing the apical tip of the capsule (wet state), *A. hoffmannseggiana* typical form (*Steyn 2148*, PRE); F, appressed hygroscopic hairs on seed (dried state), *A. horrida* (*Steyn 1814b*, PRE). Scale bar: B, C = 2 mm, D, E = 1 mm, F = 0.5 mm.

to unfold when the seed is moistened, and it almost doubles in size as the helical thickenings relax (partly uncoil) (Figure 10). Gutterman et al. (1967) observed in *Blepharis ciliaris* that non-lignified reticulate secondary wall thickenings are found at the base of the hygroscopic hairs and annular or spiral thickenings at the tips. According to Gutterman et al. (1967, 1973), the primary wall of cells at the tip of the hygroscopic hairs hydrates rapidly and becomes mucilaginous. Gutterman et al. (1973) and Van Rheede van Oudtshoorn and Van Rooyen (1999) stated that a thick deposit covering the hairs and seed surface of *Blepharis* hydrates rapidly upon wetting and the spiral and annular secondary wall thickenings spread out in the mucilage. Seeds of *Acanthopsis* start to germinate within 24 hours after wetting (Figure 10F).

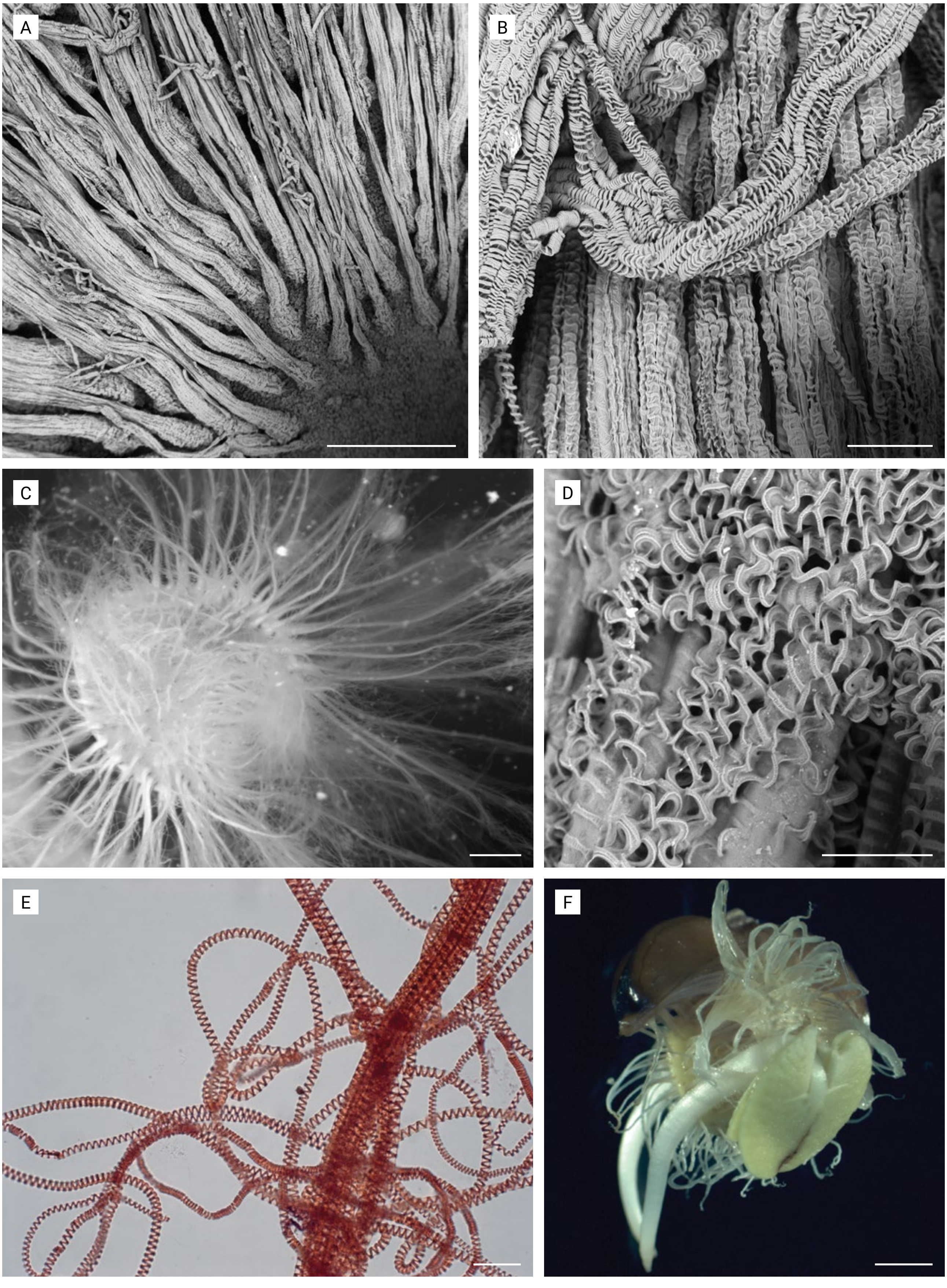

Figure 10. SEM and stereomicroscope images of *Acanthopsis* seeds, showing appressed hygroscopic hairs when dry and uncoiled mucilaginous hairs upon wetting. A and B, appressed hairs of seed (dried state), *A. dregeana* subsp. *longispina* (*Steyn 2141*, PRE); C, seed with uncoiled hairs upon wetting, *A. disperma* (*Steyn 1845*, PRE); D, uncoiled hair showing helical thickening of walls, *A. disperma* (*Steyn 1845*, PRE); E, uncoiled hairs stained with safranin, *A. disperma* (*Steyn 1845*, PRE); F, seedling, *A. hoffmannseggiana* typical form (*Steyn 2148*, PRE). Scale bar: A = 300 μm, B = 80 μm, C= 1 mm, D = 30 μm, E. 50 μm, F = 2 mm.

Discussion

The predominance of compact subshrubs in *Acanthopsis* might be explained by the generally arid and exposed habitats where this genus is found. In *A. horrida*, dense cushion-shaped shrublets, up to 600 mm high, are formed when growing among rocks on mountain slopes, but when growing in deep sandy soils of the coastal plains, the habit tends more towards an open virgate shrublet of more or less the same height than the dense cushion-shaped plants. More compact, low-growing and extensively branched plants are usually found in exposed conditions. According to Balkwill (1993), the specific growth form of plants in *Barleria* L. is often strongly correlated with the habitat in which they grow. This also appears to be the case in *Acanthopsis*.

Members of *Acanthopsis* are best adapted to warmer, drier climates (Succulent and Nama-Karoo biomes) and, therefore, virtually absent from relatively colder, wetter areas (Fynbos Biome). Some species, notably *Acanthopsis disperma* and *A. hoffmannseggiana* (both usually annuals), have a wide ecological amplitude and are capable of adapting to diverse edaphic and abiotic factors. The rest of the species (perennials) have restricted ranges, with at least eight known from only one or two subpopulations each, and are likely to have a more restricted ecological amplitude. The preponderance of perennials in *Acanthopsis* seemingly contradicts the general tendency for annuals to be favoured in hot and dry regions of the world (Poppenwimer et al. 2023). The latter authors, however, have refined this observation by showing that the prevalence of annual species is driven more by temperature and precipitation in the driest quarter, rather than by yearly means. Poppenwimer et al. (2023) also argued that future climate change may favour annuals, but impact negatively on ecosystem services provided by perennials, raising some conservation concerns considering the several perennial species with restricted ranges in *Acanthopsis*.

Floral bracts usually protect the developing flowers of a plant by forming a physical shield around it. In *Acanthopsis*, the floral bracts ending in rigid spines not only protect the flowers, but also the fruit and seed and most probably mechanically deter herbivory, notably of mammalian browsers like antelope. Spines as a defensive strategy may extend beyond larger browsers like antelope, as research indicates that spines also serve as an effective defence against browsing/herbivory by small mammals such as rodents (Cooper & Ginnett 1998). In the case of *Acanthopsis*, the safeguarding of fruit through spines would likely be advantageous, particularly given the prolonged period during which dry but still indehisced fruits are retained in old infructescences. However, it was observed that the dried, persistent bracts (including spines) soften considerably when moistened, and it is believed that species known to be browsed (e.g., *A. carduifolia* and *A. dregeana*), are being utilised in this way shortly after rains when the inflorescences are soft and more palatable. Whether coincidental consumption of the fruit in this manner holds any advantages for seed dispersal, requires further investigation.

Very little information is available on the reproductive biology of *Acanthopsis* but the similarity in corolla shape and colour among taxa may be indicative of them sharing a similar pollination biology. Pollen grains of *Acanthopsis* are sculptured (usually with a reticulate or microreticulate mesocolpium) and relatively large compared to those of *Acanthus* and *Blepharis*. Chaloner (1986) suggested that sculptured pollen grains would retain their electrostatic charge longer and, as a result, would be more adhesive to the stigma. Electrostatic charges may also play a role in the attachment of pollen grains to insect vectors (Thorp 1979; Vaknin et al. 2000). Ornamented grains (as found in nearly all species of *Acanthopsis*), therefore, have an advantage not only in its adhesion to the stigma, but also in attaching to the insect vector.

Floral traits of *Acanthopsis* show the classical syndrome for insect pollination (entomophily) (Faegri & Van der Pijl 1979; Proctor et al. 1996; Dellinger 2020). These features encompass zygomorphic flowers, characterised by a conspicuous lip that may function as a landing site, a slender corolla tube and well-defined nectar guides. The prevalent bluish hue of the corollas may serve as a visual attractant, complemented by the provision of both nectar and possibly pollen as rewards. However, the observation that the anthers do not release the pollen conspicuously, suggests that nectar is the main reward; and the presenting of pollen in the direction of the corolla lip, suggests that the pollen is most probably deposited on the dorsal side of the visiting insect. The conspicuous horizontal corolla lip found in most species, suggests a landing platform and therefore a hovering insect would probably not be a primary pollinator. That the nectar is concealed within a narrow corolla tube (± 1 mm wide), suggests a pollinator with a relatively long, thin proboscis. Although bees would be the implied pollinators of *Acanthopsis* based on the predominant colours (lilac to purple) of the corollas (Corbet et al. 1991; Menzel & Schmida 1993; Gess & Gess 2010, 2014), they would not be able to reach the nectar as the corolla tube is too long and narrow.

While casual observations have noted the presence of insects from various groups visiting the flowers, the narrow and often elongated corolla tubes, with nectar primarily concentrated at the tube's base, also suggest a potential adaptation for pollination by long-proboscid insects such as tangle-veined flies (Nemestrinidae) and bee flies (Bombyllidae). *Acanthopsis tuba* has a particularly pronounced corolla tube, (15–)25–35 mm long, and is sympatric with *Lapeirousia dolomitica* Dinter (Iridaceae), a small, long-tubed geophyte (Goldblatt & Manning 2015). The latter species has pale blue to violet or lilac flowers and a perianth tube 25–35(–40) mm long and is visited (and probably pollinated) by a long-proboscid tangle-veined fly (Goldblatt 2000; Goldblatt & Manning 2015). A long-proboscid fly or bee fly could therefore also be the pollinator of *A. tuba* as the corolla lip of the latter species is more vertical than the rest of the species and would suggest a hovering insect as pollinator. Hitherto limited but noteworthy field observations have documented instances of bee flies visiting *Acanthopsis* flowers, as illustrated in Figure 8C (P. van Wyk, pers. comm. 2017; F. Grenier, pers. comm. 2018), but not yet any tangle-veined flies.

Rostás and Tautz (2010) mentioned that sticky blossoms and trichomes [as present in e.g., *A. glandulopalmata*, *A. hoffmannseggiana* (typical form) and *A. tetragona*] might be adaptations by the plant to prevent ants from robbing pollen, damaging anthers or pistils or scaring away potential pollinators (thereby preventing ant pollination). However, members of *Acanthopsis* include traits suggested to be characteristic of an ant pollination syndrome (Rostás & Tautz 2010): plants short and growing in dry, warm habitats with an abundance of foraging ants; flowers easily accessible, with little nectar and a few flowers blooming synchronously and few or relatively small pollen grains. The production of nectar, a lack of a pronounced odour, the darker purple veins on the corolla (nectar guides), and the size and sculpture of the pollen grains suggest diurnal insects (bees, ants, bee flies and fruit flies) as possible pollinators.

Plants often distribute their offspring during favourable conditions over time, to take the best advantage of unpredictable environments. The timing of seed germination is the earliest trait in plant life-history, and allows plants to regulate when and where they grow (Liu et al. 2017). The bilocular capsules of *Acanthopsis* remain covered by four sepals in the dry state, and only upon wetting do the bracts open up (diverge) and the sepals separate to expose the capsule. This antitelechoric behaviour ensures that mature capsules are retained unopened on the plant and that seeds are only dispersed when sufficient water for germination is present (Gutterman et al. 1967; Gutterman 1994; Van Rheede van Oudtshoorn & Van Rooyen 1999). Portioned dispersal ensures that even with sufficient rain, not all the seeds are dispersed with the first rainfall event of the season and a reserve for later dispersal is left (Gutterman et al. 1967; Gutterman 1994) as sepals of older fruit open in light rain, while younger ones tend to stay closed (Van Rheede van Oudtshoorn & Van Rooyen 1999). The observation that relatively young but dry fruit of *Acanthopsis* do not readily dehisce to release the seed, may also be indicative that the seeds themselves have a dormancy requirement. Seed dormancy is an important survival strategy of plants in their natural environments (Finch-Savage & Leubner-Metzger 2006).

The incidence and ecology of very fast germination (within 24 h) among flowering plants were reviewed by Parsons (2012). In species with very fast germination all the seeds may germinate within a very short time following wetting, or only a small fraction may germinate, whereas the rest would remain as a long-lived soil seed bank (Parsons 2012). In Acanthaceae, Gutterman (1972) reported that the seed of *Blepharis ciliaris* (L.) B.L.Burtt [as *B. persica* (Burm.f.) Kuntze] germinates within less than 50 minutes after wetting. Moreover, in studied species of *Blepharis* all seeds germinate at the same time (Gutterman 2002). Rapid germination is important for plant survival, especially in arid areas where rain is infrequent and where dispersed seeds are collected by ants (Gutterman 1994; Parsons 2012). A seed starts to germinate in favourable conditions, in the case of *Acanthopsis* in response to the availability of moisture. Germination is a physiologically complex process (e.g., Nonogaki et al. 2010; Rajjou et al. 2012), hence the rapid germination of *Acanthopsis* seed within 24 h after wetting is rather unusual and comprises a highly specialised adaptation, most probably to its arid environment. It remains to be established if in the case of *Acanthopsis*, all the released seeds germinate simultaneously, as in *Blepharis*.

In both *Acanthopsis* and *Blepharis*, the appressed, hygroscopic hairs on the seeds immediately start to unfold when the seeds are moistened and mucilage is produced. The mucilage binds the seed (and the future seedling) to the soil, a phenomenon known as myxospermy (Gutterman et al. 1967; Manktelow 1996; Van Rheede van Oudtshoorn & Van Rooyen 1999; Vollesen 2000), and possibly acts as a counterforce to the penetrating root (Gutterman et al. 1967, 1973). It may also help to prevent ants from collecting the seed, protect the seed from the abrasive powers of the wind during dry periods, and ensure that they germinate in the same favourable microclimate as the mother plant (Van Rheede van Oudtshoorn & Van Rooyen 1999). The mucilage could also be an initial source of moisture and nutrients for the young seedling (Gutterman et al. 1967; Gutterman et al. 1973; Vollesen 2000). According to Gutterman (1994) and Van Rheede van Oudtshoorn and Van Rooyen (1999), the mucilage could increase the buoyancy of the seed in some cases and therefore improve dispersal by water – this may well be the case in *A. disperma*, an annual species often occurring in dry, sandy washes, depressions or flats.

Environmental conditions in arid areas, as those inhabited by the genus *Acanthopsis*, are highly unpredictable. Plants adapted to these conditions have evolved an array of functional traits to enhance their chances of survival. The present contribution focuses on a select few of these traits, with discussion centred around them. Given the anticipated climate change, it is crucial to comprehend how species within these environments will react to alterations in temperature and precipitation. Kühn et al. (2021) have proposed a set of functional traits that could serve as useful indicators for predicting species responses to climate shifts. This approach operates under the assumption that there exists general relationships between traits and the environment, and that the proposed traits are closely associated with climatic conditions. However, a detailed analysis of these traits in *Acanthopsis* is not covered in this study and represents a significant avenue for future research.

Acknowledgements

The authors would like to thank the curators from different herbaria for supplying scanned images of specimens; Marinda Koekemoer, Pieter Bester and Pieter van Wyk for collecting herbarium vouchers and supplying images; Dr Hugh Glen and Dr Otto Leistner for help with Latin translations; John Roux (Farm Silverfontein) and the owners of Warmwaterberg Spa near Barrydale for permission to collect specimens on their properties; Daleen Roodt for the line drawings and Elizma Fouché for preparing the photo plates. I gratefully acknowledge the Richtersveld Cultural and Botanical Landscape for permission to collect plants; SANParks for accommodation and assistance during work in the Richtersveld and Namaqua national parks. Our grateful thanks to CapeNature, as well as the Department of Tourism, Environment and Conservation: Northern Cape, for plant collecting permits, and the Botanical Education Trust for financial support.

Competing interests

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

Authors' contributions

HMS (SANBI) performed the research and wrote the manuscript and AEvW (University of Pretoria) made conceptual contributions and edited the manuscript.

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BOTHALIA – African Biodiversity & Conservation
ISSN: (Online) 2311-9284, (Print) 0006-8241

An appraisal of the Mozambique types and endemic taxa in the Pires de Lima plant collection at the Porto Herbarium (PO, MHNC-UP)

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Dates

Submitted: 3 March 2023
Accepted: 8 December 2023
Published: 21 May 2024

How to cite this article:

Faria, M.B., Vieira, C., Viegas, S.B. & Paiva, J., 2024, 'An appraisal of the Mozambique types and endemic taxa in the Pires de Lima plant collection at the Porto Herbarium (PO, MHNC-UP)', *Bothalia* 54, a6. http://dx.doi.org/10.38201/btha.abc.v54.6

Putative type specimens of 18 taxa described from Mozambique collected by Américo Pires de Lima at the beginning of the 20th century are kept in the African collections of the Herbarium of Porto (PO) at the MHNC-UP. These specimens were not collected as part of a dedicated scientific mission, but they and the scientific studies carried out by Pires de Lima represent an important contribution to Portuguese colonial projects. During his scientific career, and despite the lack of support and specialised literature, Pires de Lima described 17 species new to science. In this work we analysed part of the material collected by Pires de Lima, kept in PO at MHNC-UP. Today, only two of the 17 taxa described by Pires de Lima remain as accepted taxa, viz. *Tephrosia reptans* var. *microfoliata* (Pires de Lima) Brummitt and *Crotalaria retusa* var. *tunguensis* (Pires de Lima) Polhill. In addition, information on *Polygala limae* Exell, named after Pires de Lima, has also been analysed as this is still accepted. Of over 300 specimens collected by Pires de Lima in the early 20th century, some 40% remain unidentified due to lack of expertise. Undoubtedly, this collection contains many other promising specimens in need of revision, taxonomic update, and other novelties that can be found even in the more ancient and inconspicuous materials.

Keywords: botanical collections, Natural History and Science Museum of University of Porto, Mozambique flora, Herbarium of the University of Porto, systematics.

Introduction

Mozambique is a botanical hotspot with five phytogeographic regions organised into communities of miombo, mopane, undifferentiated woodland and coastal mosaic (Burgess et al. 2004). In recent years, several centres of plant endemism have been recognised in Mozambique, with new taxa described at a significant rate. Mozambique includes four cross-border centres of botanical endemism, namely the Rovuma Centre, encompassing northeastern Mozambique and southeastern Tanzania (Darbyshire et al. 2019), where the province of Cabo Delgado is located, from which the botanical specimens discussed here originate.

Recent checklists of the flora of Mozambique, based on published literature, online databases and herbarium collections, recognise 5 957 species plus 605 subspecies and 537 varieties belonging to 226 families and 1 746 genera (Odorico et al. 2022). Initiatives such as the International Union for Conservation of Nature-Species Survival Commission (IUCN-SSC) Southern African Plant Specialist Group to update plant species assessments in the 2017–2020 period, and the 'Tropical Important Plant Areas: Mozambique' project, have been developed to raise awareness of the importance of Mozambique's flora (Darbyshire et al. 2019). A thorough assessment for Mozambique carried out in 2021 included 1 667 of the recorded taxa on the IUCN Red List (Odorico et al. 2022).

At the beginning of the 20th century, scientific research in Portuguese colonies witnessed a change in attitude towards the Portuguese model of colonisation, largely due to international pressure that promoted a shift from the occupation of colonial territories by 'historical right' to 'effective occupation' (Neto 2013; Pires & Fogarty 2014). These changes, reinforced by the Berlin Conference of 1884/5, required a deeper scientific knowledge of the colonised territories. The scientific investigations carried out by Américo Pires de Lima in Mozambique between 1916/17 in the Cabo Delgado Province (Pires de Lima 1933), although not strictly a scientific mission, can be placed within this paradigm of the Portuguese colonial project.

The Herbarium of the University of Porto (PO) founded in 1892, is at present part of the Natural History and Science Museum of the University of Porto (MHNC-UP) (Folhadela et al. 1993; Vieira & Viegas 2019). With almost 130 000 specimens, it is one of the three largest herbaria in Portugal. In addition to the Portuguese flora, PO houses collections of the flora of former Portuguese colonies. These include a Mozambique collection, with specimens collected by various collectors some 50 to 100 years ago. As with other African collections, they remain as the institution's backlog due to lack of expertise for identification.

Among the specimens from the PO African herbarium is the collection of Américo Pires de Lima (1886–1966), a medical doctor, professor, botanist, bacteriologist and researcher. As an academic, he was a major figure at the University of Porto, where he held prominent positions including Director of the Faculty of Sciences and the Faculty of Pharmacy at the University of Porto and the Institute of Botany (Salema 1989). In 1916, still at the beginning of his academic career at the Faculty of Sciences, he was mobilised for World War I as a lieutenant doctor in an expedition to Mozambique, and also head of the Hygiene and Bacteriology Section (Pires de Lima 1933). Although this was a military mission, Pires de Lima was commissioned by two professors from the University of Porto, and reinforced by a ministerial decree, to take advantage of the trip to Mozambique to carry out studies on the flora, fauna and anthropology of the region where he was stationed, without disruption to his military service (Salema 1989).

Although Pires de Lima was not an expert in African botany, he endeavoured to collect in Mozambique, to analyse some of this material and to proceed with the identification of some of the specimens. He did this without an adequate specialised library and, according to his testimony, identified specimens by comparison (Pires de Lima 1950). The classification process was partly carried out with the help of Gonçalo Sampaio (1865–1937; University of Porto) and Júlio Henriques (1838–1928; University of Coimbra) (Pires de Lima 1921), the two best-trained botanists in Portugal at the time. It is also known that Pires de Lima intended to send the specimens to experts at Kew (Pires de Lima 1950). Some of the Pires de Lima specimens are type specimens of lichens or vascular plants from Mozambique referred to in the works of Vainio and Pires de Lima (Vainio 1930; Pires de Lima 1921, 1922, 1924; Paz-Bermúdez 2004), published in the Portuguese scientific journals available at the time, which contained much taxonomic content (Boletim da Sociedade Broteriana and Brotéria journals). Pires de Lima is known to have published at least 20 vascular plant names during the period between 1921 and 1924 (Figueiredo et al. 2018).

Initiatives such as Flora Zambesiaca and the work evaluating endemism in Mozambique and the checklist of Vascular Plants of Mozambique (Mendonça & Wild 1960, Darbyshire et al. 2019, Odorico et al. 2022), allowed us to verify that the locations of Pires de Lima's collections correspond to areas that were little-known to European botany, which highlights the value of these collections.

Currently, the coastal region of the province of Cabo Delgado is identified as having high botanical value in the country and is recommended as a strategic conservation priority (Odorico et al. 2022). Added to this fact are the current scenarios of armed conflict, affecting the lives of populations and also resulting in the destruction of habitats. Pires de Lima's collection from a period of about 100 years ago, covers different types of habitats, and constitutes an important reference of the region's previous floristic cover, for habitat conservation and restoration projects.

This paper aims to document some of the types of the Mozambique vascular collection housed at PO, and to promote understanding and awareness of the importance of the permanent review of biological collections in systematics.

Materials and methods

The need for taxonomic and nomenclatural adjustments of the PO Mozambican types was identified in the context of an inventory following the project: IAPT REPORT Small Collections Grants – Grant Application (grant round 2019–20: African Backlog at PO Herbarium: uncovering 20th-century collectors and specimens from unofficial African botanical missions) and studied in the context of work placement (Faria 2021). These two processes made it possible to access PO and to search, organise, photograph or catalogue the African and, in particular, the Mozambican collections. In time, it was possible to complete the recognition of the backlog of collections that had been unrecognised for several decades. We also found that the Pires de Lima collection is accompanied by documentation, such as notebooks with descriptions, inventories and publications and we were able to photograph specimens (Canon EOS 6D MARK II camera).

Results

Of the 324 vascular specimens collected by Pires de Lima, 59% were identified to at least family level, with the most represented families being Fabaceae, followed by Cyperaceae. A total of 175 of these specimens have been identified and published with collector numbers (Pires de Lima 1921, 1922, 1924), but 149 remain unidentified until today. Although there have been some evaluations of specimens in this vascular plant collection by Kew and British Museum staff or researchers (Arthur Wallis Exell, Richard Kenneth Brummitt, Jane Browning, Roger Marcus Polhill) or other sporadic studies by African flora specialists (Jorge Paiva, António Rocha da Torre, Simone Balle, Franciscus Jozef Breteler and Paul Goetghebeur), these types needed a taxonomic revision to support the global databases that still present Pires de Lima names as unresolved.

In total, 18 of the 324 specimens in the collection of Américo Pires de Lima (1921, 1922 and 1924) were identified as 'typus' by Pires de Lima or by other authors studying the collection. These type specimens were collected between 1916 and 1917, 16 by Américo Pires de Lima himself and two by his friend, Lieutenant Romualdo Tavares (Pires de Lima 1921, 1922, 1924), also in military service.

Types

The vascular plant specimens from the Pires de Lima collection that have been accessed and studied, and previously marked as types, are the following 18 taxa, listed in alphabetical order by family:

Acanthaceae

Hygrophila palmensis Pires de Lima in Boletim da Sociedade Broteriana, Sér. 2, 2: 149 (1924). TYPE: MOZAMBIQUE, Tungue, near Palma, 14 Aug. 1916, *Pires de Lima 26* (POV-69221) [1 specimen] = **Hygrophila auriculata** (Schumach.) Heine in Kew Bulletin 16 (2): 172 (1963).

Distribution: Mozambique

Notes: These specimens were initially designated by Pires de Lima as *Hygrophila palmensis* Pires de Lima (type specimen). According to Plants of the World Online (POWO), *Hygrophila palmensis* Pires de Lima co-exists with *Hygrophila auriculata* (Schumach.) Heine in Mozambique. Accordingly, in 2022, one of the authors of this manuscript (J. Paiva) reviewed the specimen as *Hygrophila auriculata* (Schumach.) Heine. (Figure 1).

Amaranthaceae

Achyranthes asperoides Pires de Lima in Brotéria, Série Botânica, 19, 3: 116 (1921). TYPE: MOZAMBIQUE, Cabo Delgado, surroundings of Palma, 8 Feb. 1917 and 4 Mar. 1917, *Pires de Lima 118* (POV-69282; POV-69283) [2 specimens] = **Achyranthes aspera** L., Species plantarum 1: 204 (1753a); Townsend: 101 (1985); Townsend: 106 (1988). *A. aspera* var. *sicula* L., Species plantarum 1: 204 (1753a); Townsend: 104 (1985); Townsend: 109 (1988).

Distribution: A. aspera var. *sicula* L. distribution includes Africa, Mediterranean to West Asia and Arabian Peninsula, India.

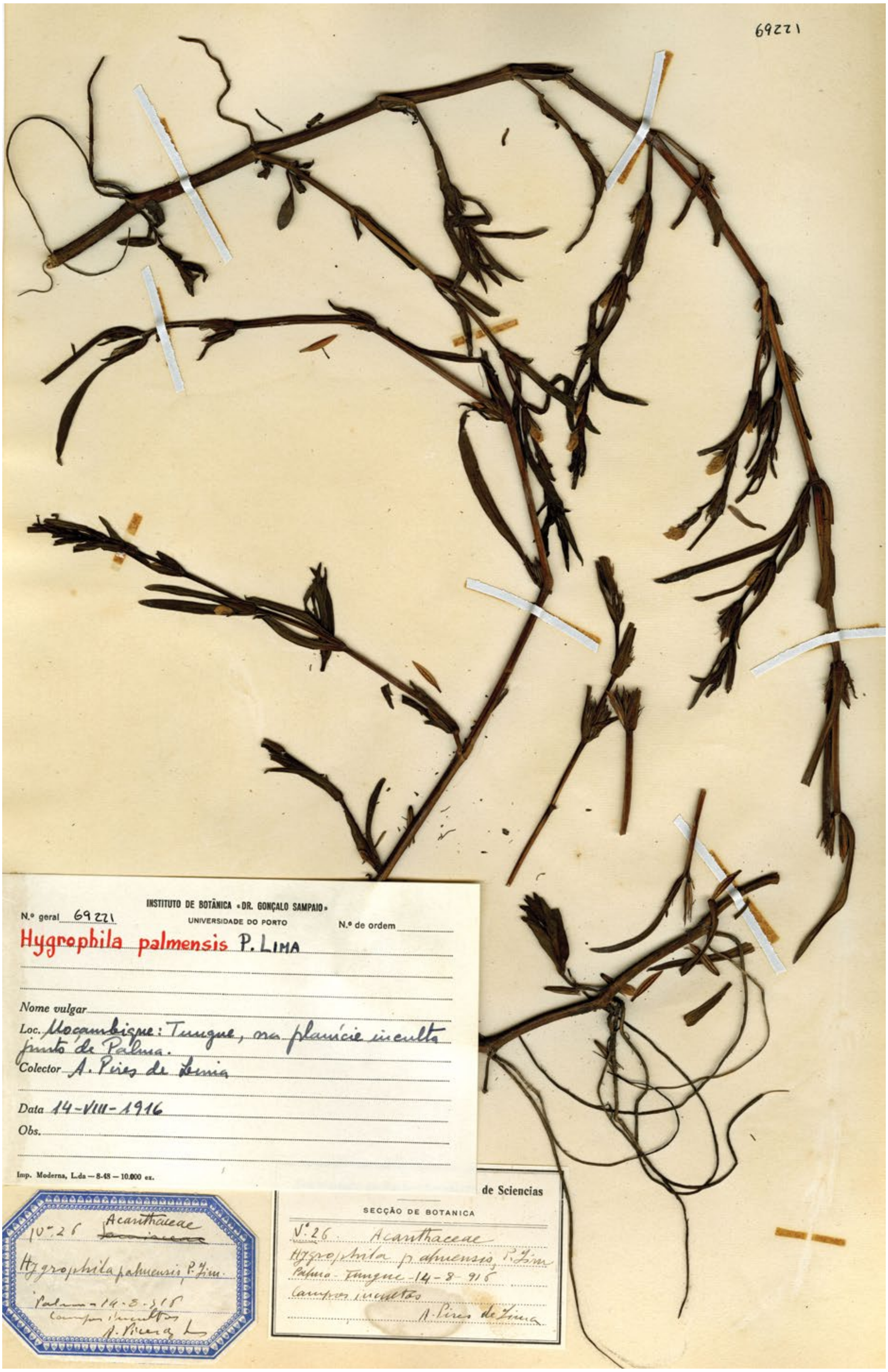
Notes: These specimens were initially designated by Pires de Lima as *Achyranthes asperoides* Pires de Lima (type specimen). According to the POWO, *Achyranthes asperoides* Pires de Lima is recognised as a synonym of *Achyranthes aspera* L. var. *aspera*. Until 2022, no other researcher examined this specimen, which one of the authors of this manuscript (J. Paiva) identified as *Achyranthes aspera* L. var. *sicula* L. (Figure 2).

Cleomaceae

Pedicellaria glandulosa Pires de Lima in Brotéria, Série Botânica, 19, 3: 117 (1921). TYPE: MOZAMBIQUE, Cabo Delgado, near Palma, 9 Aug. 1916, *Pires de Lima 9* (POV-68998, POV-69297) [2 specimens] = **Cleome gynandra** L., Species plantarum 2: 671 (1753b); Figueiredo & Smith: 55 (2008). *Gynandropsis gynandra* (L.) Briq. 17: 382 (1914); Wild: 205, tab. 31 (1960); Elffers et al.: 18, fig. 3 (1964).

Distribution: Cleome gynandra L. is native in tropical and subtropical Africa, Madagascar and tropical Asia; introduced to SW Europe, Central America and northern South America.

Notes: These specimens were initially labelled by Pires de Lima as *Pedicellaria glandulosa* Pires de Lima (type specimens). However, according to the POWO, *Pedicellaria glandulosa* Pires de Lima is currently considered an unplaced name that cannot be accepted or synonymised. In 2022, one of the authors of this manuscript (J. Paiva) argues that Pires de Lima misidentified it and identifies it as *Cleome gynandra* L. (Figure 3).



69221

INSTITUTO DE BOTÂNICA «DR. GONÇALO SAMPAIO»
UNIVERSIDADE DO PORTO
N.º geral 69221
N.º de ordem
Hygrophila palmensis P. Lima
Nome vulgar
Loc. Moçambique: Tungue, na planície inculta junto de Palma.
Colector A. Pires de Lima
Data 14-VIII-1916
Obs.
Imp. Moderna, L.da — 8-48 — 10.000 ex.

N.º 26 Acanthaceae ~~[illegible]~~
Hygrophila palmensis P. Lim.
Palma - 14-8-916
Campos incultos
A. Pires de L.

de Sciencias
SECÇÃO DE BOTANICA
N.º 26 Acanthaceae
Hygrophila palmensis P. Lim
Palma - Tungue - 14-8-916
Campos incultos
A. Pires de Lima

Figure 1. *Hygrophila palmensis* Pires de Lima. Specimen POV-69221.

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N.º geral 69282
N.º de ordem
Achyranthes asperoides P. LIMA
Nome vulgar
Loc. Moçambique: na planície inculta junto de Palma.
Colector A. Pires de Lima
Data 26-II-1917
Obs.
Imp. Moderna, L.da — 8-48 — 10.000 ex.

Figure 2. *Achyranthes asperoides* Pires de Lima. Specimen POV-69282.

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N.º geral
N.º de ordem 68998

Pedicellaria glandulosa P. LIMA

Nome vulgar
Loc. Moçambique: terrenos incultos junto da povoação de Palma
Colector A. Pires de Lima
Data 9-VIII-1916
Obs. N.º 9

Imp. Moderna, L.da — 8-48 — 10.000 ex.

Figure 3. *Pedicellaria glandulosa* Pires de Lima. Specimen POV-68998.

Colchicaceae

Gloriosa sampiana Pires de Lima in Brotéria, Série Botânica, 19, 3: 112 (1921). TYPE: MOZAMBIQUE, Madai, 3 Apr. 1917, *Pires de Lima 173* (POV-69286, POV-68979) [2 specimens] = *Gloriosa simplex* L., Mantissa plantarum: 62 (1767); Maroyi: 122, Fig. 6.13 (2012); Thiombiano et al.: 36 (2012).

Distribution: Gloriosa simplex L. is widespread in tropical and southern Africa.

Notes: These specimens were initially designated by Pires de Lima as *Gloriosa sampiana* Pires de Lima (type specimen). According to the POWO, **Gloriosa sampiana** Pires de Lima is recognised as a synonym of *Gloriosa simplex* L. Until 2022, no other researcher examined this specimen, which one of the authors of this manuscript (J. Paiva) identified as *Gloriosa simplex* L. (Figure 4).

Cyperaceae

Fimbristylis rhizomatosa Pires de Lima in Boletim da Sociedade Broteriana, Sér. 2, 2: 134 (1924). TYPE: MOZAMBIQUE, Palma, Quionga, 8 Nov. 1916, *Pires de Lima 52* (POV-62233, POV-62234) [2 specimens] = **Bulbostylis burchellii** (Ficalho & Hiern) C.B.Clarke: 612 (1894); Figueiredo & Smith: 178 (2008).

Distribution: Bulbostylis burchellii is native from Tanzania to South Africa.

Notes: These specimens were initially labelled by Pires de Lima as *Fimbristylis rhizomatosa* Pires de Lima (type specimens). In July 1991, Paul Goetghebeur reviewed the specimens as *Bulbostylis burchellii* (Ficalho & Hiern) C.B.Clarke. In 2022, one of the authors of this manuscript (J. Paiva) also agreed that Pires de Lima misidentified the specimens and agreed with P. Goetghebeur, naming them *Bulbostylis burchellii*. (Figure 5).

Fimbristylis elongata Pires de Lima in Boletim da Sociedade Broteriana, Sér. 2, 2: 133 (1924). TYPE: MOZAMBIQUE, Palma, Tungue, 21 Sept. 1917, *Pires de Lima 32* & *145* (POV-68955, POV-69316, POV-68954) [3 specimens] = **Bulbostylis contexta** (Nees) Bodard in Annales de la Faculté des sciences, Université de Dakar 9: 77 (1963); Figueiredo & Smith: 178 (2008).

Distribution: Bulbostylis contexta is native to Ethiopia, South Africa and Madagascar.

Notes: These specimens were initially labelled by Pires de Lima as *Fimbristylis elongata* Pires de Lima (type specimens). In July 1991, Paul Goetghebeur reviewed the specimens as *Bulbostylis contexta* (Nees) Bodard. In 2022, one of the authors of this manuscript (J. Paiva) also agreed that Pires de Lima misidentified the specimens and agreed with P. Goetghebeur, naming them *Bulbostylis contexta*. (Figure 6).

Fimbristylis longebracteata Pires de Lima in Boletim da Sociedade Broteriana, Sér. 2, 2: 134 (1924). TYPE: MOZAMBIQUE, surroundings of Palma, 10 Feb. 1917, *Pires de Lima 104* (POV-62232) [1 specimen] = **Bulbostylis hispidula** (Vahl) R.W.Haines, Sedges & Rushes E. Afr. 3: p.[1] (1983); Figueiredo & Smith: 178 (2008).

Distribution: Bulbostylis hispidula is native to the tropics and subtropics and the Caucasus.

Notes: These specimens were initially labelled by Pires de Lima as *Fimbristylis longebracteata* Pires de Lima (type specimens). In July 1991, Paul Goetghebeur reviewed the specimens as *Bulbostylis hispidula* (Vahl) R.W.Haines. In 2022, one of the authors of this manuscript (J. Paiva) also agreed that Pires de Lima misidentified the specimens and agreed with Goetghebeur, naming them *Bulbostylis hispidula*. (Figure 7).

Fabaceae

Abrus gracilis Pires de Lima in Brotéria, Série Botânica, 19, 3: 127 (1921). TYPE: MOZAMBIQUE, Cabo Delgado, surroundings of Palma, 8 May 1917, *Pires de Lima 257* (POV-69004; POV-69301; Kew photo negative 7527; 7526) [2 specimens] = **Abrus melanospermus** subsp. **tenuiflorus** (Benth.) D.K.Harder in Novon 10: 124 (2000); Timberlake et al.: 216 (2007).

Distribution: Abrus melanospermus subsp. *tenuiflorus* is native to tropical Africa and Madagascar.

Notes: These specimens were initially labelled by Pires de Lima as *Abrus gracilis* Pires de Lima (type specimens). In March 1960, F.J. Breteler reviewed the specimens as *Abrus fruticulosus* Wall. ex Wight & Arn. In October 1961, G. Nertcourt reviewed the specimens as *Abrus pulchellus* subsp. *tenuiflorus* (Spruce ex Benth.) Verdc. In 2022, one of the authors of this manuscript (J. Paiva) also agreed that Pires de Lima misidentified the specimens, and agreed with G. Nertcourt, naming them as *Abrus melanospermus* subsp. *tenuiflorus* (Spruce ex Benth.) D.K.Harder, the currently accepted name for the synonym of *Abrus pulchellus* subsp. *tenuiflorus* (Spruce ex Benth.) Verdc. (Figure 8).

Abrus tunguensis Pires de Lima in Brotéria, Série Botânica, 19, 3: 127 (1921). TYPE: MOZAMBIQUE, Cabo Delgado, surroundings of Palma, 8 Feb. 1917 and 4 Mar. 1917, *Pires de Lima 94* and *134* (POV-69285; POV-69284; Kew photo negative

INSTITUTO DE BOTÂNICA «DR. GONÇALO SAMPAIO»
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N.º geral
N.º de ordem 68979
Gloriosa Sampaiana P. LIMA
Nome vulgar
Loc. Moçambique: Madai, próximo do rio Rovuma.
Colector Romualdo Tavares
Data 3-IV-1917
Obs. Nº173
Imp. Moderna, L.da — 8-48 — 10.000 ex.

Figure 4. *Gloriosa sampiana* Pires de Lima. Specimen POV-68979.

Bulbostylis burchellii 62234
(Ficalho & Hiern) C.B.
Clarke

DET. J. Browning Sept 2016

INSTITUTO DE BOTÂNICA «DR. GONÇALO SAMPAIO»
UNIVERSIDADE DO PORTO
N.º geral 62234
N.º de ordem 18-A-e
Fimbristylis rhizomatosa P. Lima
Nome vulgar
Loc. Moçambique: no mato junto da estrada de Palmá a Quionga.
Colector A. Pires de Lima
Data 8-XI-1916
Obs. Número 52
Imp. Moderna, L.da — 8-48 — 10.000 ex.

= Bulbostylis burchellii 62234
(Ficalho & Hiern) C.B. Clarke
Determinavit P. Goetghebeur, 7-1991
RL

Universidade do Porto — Faculdade de Sciencias
SECÇÃO DE BOTANICA
N.º 52 Cyperaceae
Fimbristylis rhizomatosa, P. Lim.
Estrada de Palma a Quionga, 8-11-916
(Mato)
A. Pires de Lima

Figure 5. *Fimbristylis rhizomatosa* Pires de Lima. Specimen POV-62234.

= Bulbostylis contexta (Nees) Bodard
68954

Determinavit P. Goetghebeur, 7-1991

RL

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N.º geral 68954
N.º de ordem 18-A-b

Fimbristylis elongata P. LIMA

Nome vulgar
Loc. Moçambique: Palma, Tungue, no mato dos arredores.
Colector A. Pires de Lima
Data 18-III-1917
Obs. N.º 145; Há duas folhas de Herbário

Imp. Moderna, L.da — 8-48 — 10.000 ex.

Universidade do Porto — Faculdade de Sciencias
SECÇÃO DE BOTANICA

N.º 145 - Cyperaceae
Fimbristylis elongata, P. Lima
Palma - Tungue - 18-3-917
(Mato)
A. Pires de Lima

Figure 6. *Fimbristylis elongata* Pires de Lima. Specimen POV-68954.

Bulbostylis hispidula (Vahl) R.W. Haines
62232
DET. J. Browning Sept 2016

104

= Bulbostylis hispidula (Vahl) Haines 62232
Determinavit P. Goetghebeur 7-1991
RL

INSTITUTO DE BOTÂNICA «DR. GONÇALO SAMPAIO»
UNIVERSIDADE DO PORTO
N.º geral 62232
N.º de ordem 18-A-d
Fimbristylis longebracteata P. LIMA
Nome vulgar
Loc. Moçambique: Palma, no mato dos arredores.
Colector A. Pires de Lima
Data 10-II-1917
Obs.
Imp. Moderna, L.da — 8-48 — 10.000 ex.

N:104 Cype
Fimbristylis longeb
Palma 10-2-1

Figure 7. *Fimbristylis longebracteata* Pires de Lima. Specimen POV-62232.

KEW NEGATIVE
No. 7526
DATE - 8 NOV 1965
INTLS.

69301 69004 DUP

I do not agree that this is A. fruticulosus.
Abrus pulchellus Thw. subsp. tenuiflorus (Benth.) Verdc. in ch.
Determinavit B Verdcourt Oct. 1965

HERBARIUM VADENSE - WAGENINGEN
Abrus fruticulosus Wall. ex W.& A.
det. F. J. Breteler 25 March 1960

INSTITUTO DE BOTÂNICA «DR. GONÇALO SAMPAIO»
UNIVERSIDADE DO PORTO
N.º geral 69301
N.º de ordem 69004 DUP
Abrus gracilis P. LIMA
Nome vulgar
Loc. Moçambique: arredores de Palma, no mato.
Colector A. Pires de Lima (dupl. 257).
Data 8-V-1917
Obs.
Imp. Moderna, L.da — 8-48 — 10.000 ex.

Figure 8. *Abrus gracilis* Pires de Lima. Specimen POV-69301.

7524; 7525) [2 specimens] = **Abrus precatorius** subsp. **africanus** Verd. in Mitteilungen der Botanischen Staatssammlung München 7: 328 (1970a); Verdcourt: 241 (1970b); Verdcourt: 114 (1971); Harder: 211 (2007).

Distribution: Abrus precatorius subsp. *africanus* is native to tropical Africa; introduced and naturalised in many regions of tropical Africa, South Africa, Seychelles, Madagascar, Mauritius, into North, Central and South America, Australia and Asia (from China to SE Asia and the Philippines).

Notes: These specimens were initially labelled by Pires de Lima as *Abrus tunguensis* Pires de Lima (type specimens). In March 1960, F.J. Breteler reviewed the specimens as *Abrus precatorius* L. In October 1961, G. Nertcourt reviewed the specimens as *Abrus precatorius* subsp. *africanus* Verdc. In 2022, one of the authors of this manuscript (J. Paiva) also agreed that Pires de Lima misidentified the specimens, and agreed with G. Nertcourt, naming them as *Abrus precatorius* subsp. *africanus* Verdc. (Figure 9).

Baphia mocimboensis Pires de Lima in Brotéria, Série Botânica, 19, 3: 120 (1921). TYPE: MOZAMBIQUE, Cabo Delgado, Mocimboa da Praia, Ponta Vermelha, 7 Sept. 1917, *Pires de Lima 265* (POV-69302; POV-69005; Kew photo negative 6705; 6704) [2 specimens] = **Baphia macrocalyx** Harms in Botanische Jahrbücher für Systematik 40,1: 33, fig.3 (1907); Brummitt et al.: 43 (2007).

Distribution: Baphia macrocalyx is native to **s**outh of Tanzania and north of Mozambique.

Notes: These specimens were initially labelled by Pires de Lima as *Baphia mocimboensis* Pires de Lima (type specimens). In July 1964, R.K. Brummitt reviewed the specimens as *Baphia macrocalyx* Harms. In 2022, one of the authors of this manuscript (J. Paiva) also agreed that Pires de Lima misidentified the specimens, and agreed with R.K. Brummitt, naming them as *Baphia macrocalyx* Harms (Figure 10).

Crotalaria tunguensis Pires de Lima in Brotéria, Série Botânica, 19, 3: 120 (1921). TYPE: MOZAMBIQUE, Cabo Delgado, surroundings of Palma, 14 Apr. 1917, *Pires de Lima 204* (POV-69308; POV-69022; Kew photo negative 7674; 7675) [2 specimens] ≡ **Crotalaria retusa** var. **tunguensis** (Pires de Lima) Polhill in Kew Bulletin 21: 311 (1968); Polhill: 958 (1971).

Distribution: Crotalaria retusa var. *tunguensis* is native to Somalia, Kenya, Tanzania and Mozambique.

Notes: These specimens were initially labelled by Pires de Lima as *Crotalaria tunguensis* Pires de Lima (type specimens). In 1965, R.M. Polhill reviewed the specimens as *Crotalaria retusa* var. *tunguensis* (Pires de Lima) Polhill. In 2022, one of the authors of this manuscript (J. Paiva) also agreed with R.M. Polhill, and named them as *Crotalaria retusa* var. *tunguensis* (Pires de Lima) Polhill (Figure 11).

Cracca incana (Roxb.) Pires de Lima in Brotéria, Série Botânica, 19, 3: 124 (1921). TYPE: MOZAMBIQUE, surroundings of Palma, 4 May 1917 and 12 Apr. 1917, *Pires de Lima 237* and *197* (POV-69018; POV-69019) [2 specimens] ≡ **Tephrosia villosa** subsp. **ehrenbergiana** (Schweinf.) Brummitt in Flora Zambesiaca 3, 3: 136, Fig. 3.3.25 (2007).

Distribution: Tephrosia villosa subsp. *ehrenbergiana* is native to Ethiopia to South Africa, Angola, Namibia and Madagascar.

Notes: These specimens were initially labelled by Pires de Lima *Cracca incana* (Roxb.) Pires de Lima (type specimens). In 1966, R.K. Brummitt reviewed the specimens as *Tephrosia villosa* subsp. *ehrenbergiana* (Schweinf.) Brummitt (homotypic synonym). In 2022, one of the authors of this manuscript (J. Paiva) agreed with R.K. Brummitt, and maintained the identification as *Tephrosia villosa* subsp. *ehrenbergiana* (Schweinf.) Brummitt (Figure 12).

Cracca bracteolata var. *microfoliata* Pires de Lima in Boletim da Sociedade Broteriana Sér. 2, 2: 137 (1924). TYPE: MOZAMBIQUE, near Palma, 24 Aug. 1916, *Pires de Lima 34* (POV-69017) [1 specimen] ≡ **Tephrosia reptans** var. **microfoliata** (Pires da Lima) Brummitt in Boletim da Sociedade Broteriana Sér. 2, 41: 287 (1968). [*Cracca bracteolata* sensu Pires de Lima in Brotéria, Série Botânica,19, 3: 123 (1921)].

Distribution: native range for *Tephrosia reptans* var. *microfoliata* is northern Mozambique.

Notes: These specimens were initially labelled by Pires de Lima as *Cracca bracteolata* var. *microfoliata* Pires de Lima (type specimens). In 1966, R.K. Brummitt renamed the specimens as *Tephrosia reptans* var. *microfoliata* (Pires da Lima) Brummitt (homotypic synonym). In 2022, one of the authors of this manuscript (J. Paiva) also agreed with R.K. Brummitt, and maintained the identification as *Tephrosia reptans* var. *microfoliata* (Pires da Lima) Brummitt (Figure 13).

Loranthaceae

Loranthus romualdensis Pires de Lima in Brotéria, Série Botânica, 19, 3: 114 (1921). TYPE: MOZAMBIQUE, Madai, 11 May 1917, *Pires de Lima 260* (POV-68985) [1 specimen] = **Agelanthus sansibarensis** (Engl.) Polhill & Wiens in Lebrun & Stork, Énumération des plantes à fleurs d›Afrique tropicale 2: 165 (1992); Polhill & Wiens: 166, photo 63,

Figure 9. *Abrus tunguensis* Pires de Lima. Specimen POV-69284.

INSTITUTO DE BOTÂNICA «DR. GONÇALO SAMPAIO»
UNIVERSIDADE DO PORTO
N.º geral
N.º de ordem 69005
Baphia mocimboensis P. LIMA
Nome vulgar
Loc. Moçambique: Mocímboa da Praia, Ponta Vermelha, no mato
Colector A. Pires de Lima
Data 7-IX-1917
Obs. Nº 265
Imp. Moderna, L.da — 8-48 — 10.000 ex.

Nº 265 [illegible]
Corola rosada. Estandarte com mancha amarela. Arbusto de pequeno porte.
Ponta Vermelha
- 7-9-917
Baphia mocimboensis, P. Lim.

Figure 10. *Baphia mocimboensis* Pires de Lima. Specimen POV-69005.

KEW NEGATIVE
No. 7675
DATE 16 DEC 1965
INTLS.

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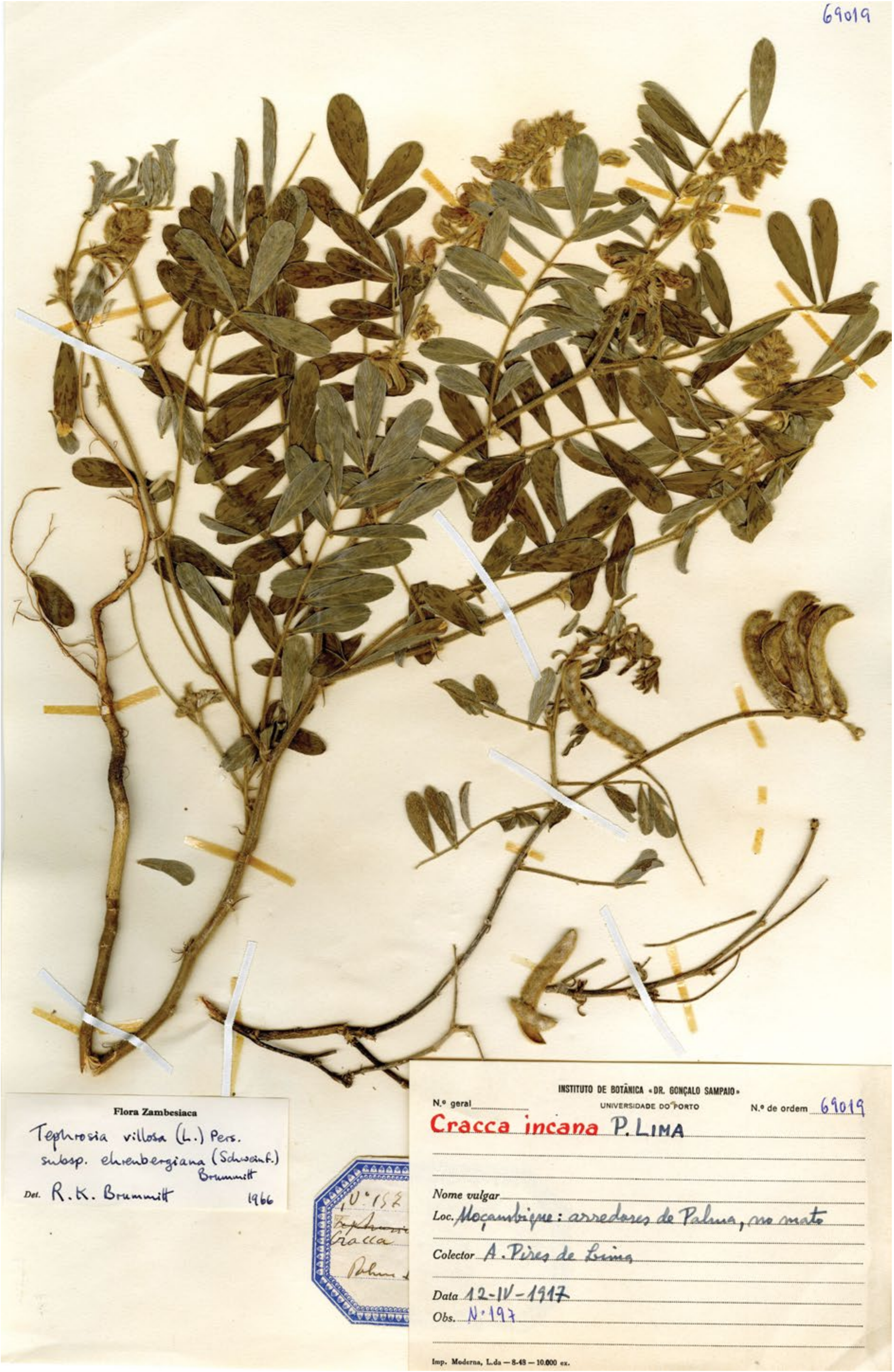
UNIVERSIDADE DO PORTO
N.º geral
N.º de ordem 69022
Crotalaria tunguensis P. LIMA
Nome vulgar
Loc. Moçambique: arredores de Palma, no mato.
Colector A. Pires de Lima
Data 14-IV-1917
Obs. N.º 204
Imp. Moderna, L.da — 8-48 — 10.000 ex.

Figure 11. *Crotalaria tunguensis* Pires de Lima. Specimen POV-69022.



69019

Flora Zambesiaca

Tephrosia villosa (L.) Pers.
subsp. ehrenbergiana (Schweinf.) Brummitt
Det. R.K. Brummitt 1966

Cracca

INSTITUTO DE BOTÂNICA «DR. GONÇALO SAMPAIO»
UNIVERSIDADE DO PORTO
N.º geral
N.º de ordem 69019
Cracca incana P. LIMA
Nome vulgar
Loc. Moçambique: arredores de Palma, no mato
Colector A. Pires de Lima
Data 12-IV-1917
Obs. N°197
Imp. Moderna, L.da — 8-48 — 10.000 ex.

Figure 12. *Cracca incana* (Roxb.) Pires de Lima. Specimen POV-69019.

Figure 13. *Cracca bracteolata* var. *microfoliata* Pires de Lima. Specimen POV-69017.

fig. 14A (1998); Polhill & Wiens: 60 (1999); Polhill & Wiens: 153 (2006).

Distribution: Agelanthus sansibarensis is native to Somalia, Kenya, Tanzania and Mozambique.

Notes: These specimens were initially labelled by Pires de Lima as *Loranthus romualdensis* Pires de Lima. In 1962, S. Balle reviewed the specimens as *Englerina inaequilatera* (Engl.) S.Balle var. *swynnertonii* (Sprague) S.Balle. In 2022, one of the authors of this manuscript (J. Paiva) reviewed the specimen and named it as *Agelanthus sansibarensis* (Engl.) Polhill & Wiens (Figure 14).

Malvaceae

Hibiscus henriquesii Pires de Lima in Brotéria, Série Botânica, 19, 3: 138 (1921). TYPE: MOZAMBIQUE, Cabo Delgado, surroundings of Palma, 14 Aug. 1916, *Pires de Lima 24* (POV-69155, POV-69156) [2 specimens] = **Hibiscus cannabinus** L., Systema naturae 10, 2: 1149 (1759); Exell: 441 (1961); Verdcourt & Mwachala: 41 (2009).

Distribution: Hibiscus cannabinus L. is widespread in tropical and subtropical Africa and extending to India (as an introduced species).

Notes: These specimens were initially labelled by Pires de Lima as *Hibiscus henriquesii* Pires de Lima (type specimens). In 1958, A. Exell, Brummitt reviewed the specimens as *Hibiscus cannabinus* L. In 2022, one of the authors of this manuscript (J. Paiva) agreed with A. Exell, and maintained the identification as *Hibiscus cannabinus* L. (Figure 15).

Orobanchaceae

Striga diversifolia Pires de Lima in Brotéria, Série Botânica, 20,1: 6 (1922). TYPE: MOZAMBIQUE, near Palma, 9 Aug. 1916 & 14 Aug. 1916, *Pires de Lima 83 & 27* (POV-69211, POV-69212) [2 specimens] = **Striga asiatica** (L.) Kuntze, Revisio generum plantarum 2: 466 (1891); Philcox: 134 (1990).

Distribution: native range for *Striga asiatica* is Africa to the Arabian Peninsula.

Notes: These specimens were initially labelled by Pires de Lima as *Striga diversifolia* Pires de Lima. In 2022, one of the authors of this manuscript (J. Paiva) reviewed the specimen and named it as *Striga asiatica* (L.) Kuntze (Figure 16).

Polygalaceae

Polygala limae Exell in Boletim da Sociedade Broteriana, Sér. 2, 31: 5 (1957); Exell: 312 (1960); Paiva: 60 (1961); Paiva: 241, tab. 45, fig. g (1998). TYPE: MOZAMBIQUE, Mocimboa da Praia, Ponta Vermelha, 12 Sept. 1917, *Pires de Lima 276* (POV-69000, holo.; POV-69314, POV-69769, iso.).

Distribution: Polygala limae is endemic to north-eastern Mozambique.

Notes: Initially this specimen remained unlabelled by Pires de Lima, who only attributed the name of the family to the specimen (Polygalaceae). In 1956, A. Exell identified the specimen as *Polygala limae* Exell. In 2000, one of the authors of this manuscript (J. Paiva) reviewed the specimen and agreed with the status of this specimen as the holotype of the name *Polygala limae* Exell, an opinion he maintains until today. J. Paiva has revisited the region where the type material was collected, but was unable to relocate additional material of *P. limae*. *Polygala limae* Exell is very similar to *P. goetzei* Gürke but appears to be an annual, whereas *P. goetzei* is a perennial, and has smaller flowers and fruits than *P. goetzei*. As there is only the type material, more material is needed to assess whether they are two species (Figure 17).

Rubiaceae

Oldenlandia prostrata Pires de Lima in Boletim da Sociedade Broteriana, Sér. 2, 2: 151 (1924). TYPE: MOZAMBIQUE, Cabo Delgado, surroundings of Palma, 22 Apr. 1917, *Pires de Lima 219* (POV-69231, POV-69232) [2 specimens] = **Oldenlandia affinis** subsp. **fugax** (Vatke) Verdc. in Kew Bulletin 30,2: 293 (1975); Verdcourt: 292, Fig. 41, 15 (1976); Figueiredo & Smith: 145 (2008).

Distribution: Oldenlandia affinis subsp. *fugax* is native to tropical and South Africa, Comoros and Madagascar.

Notes: These specimens were initially labelled by Pires de Lima as *Oldenlandia prostrata* Pires de Lima. In 2022, one of the authors of this manuscript (J. Paiva) reviewed the specimen and synonymised to *O. affinis*, but to the subspecies *fugax* (Vatke) Verdc., the subspecies of *Oldenlandia* present in Mozambique (Figure 18).

Discussion

In the Pires de Lima collection, we found specimens marked as types representing 18 taxa names. Among these, only three taxa are presently acknowledged, viz. *Crotalaria tunguensis* Pires de Lima = *C. retusa* var. *tunguensis* (Pires de Lima) Polhill, *Tephrosia reptans* var. *microfoliata* (Pires da Lima) Brummitt and *Polygala limae* Exell.

A recent study focusing on endemic species from Mozambique (Darbyshire et al. 2019) mentions three endemic taxa collected by Pires de Lima: *Polygala limae*

68985

Nº 260 - Loranthaceae

Corola avermelhada. Estames com filetes verdes e anteras amarelas.
Madai
11-5-917 R. Tavares
Loranthus romualdensis, P. Lima.

INSTITUTO DE BOTÂNICA «DR. GONÇALO SAMPAIO»
UNIVERSIDADE DO PORTO

N.º geral
N.º de ordem 68985

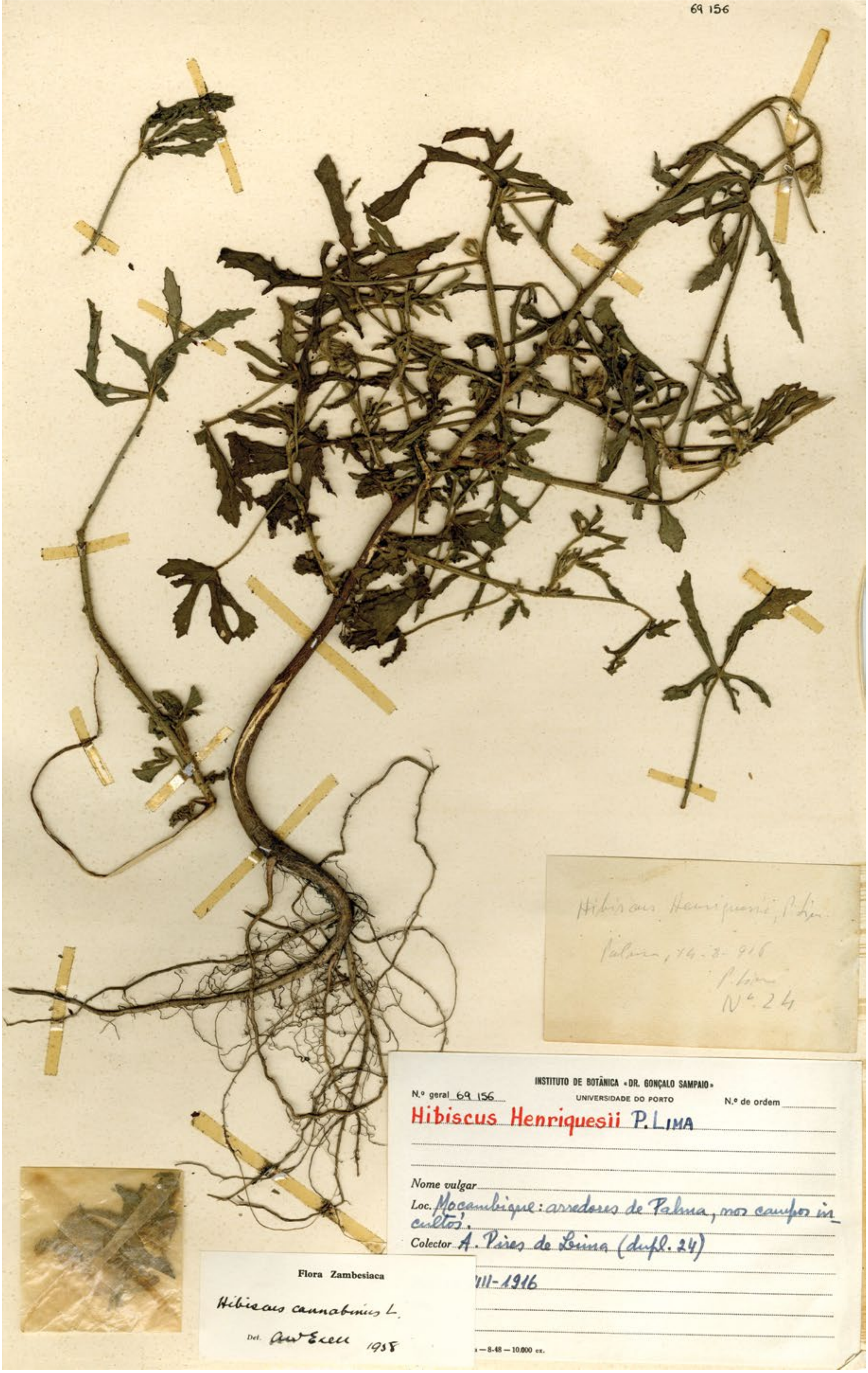
Loranthus Romualdoi P. Lima

Nome vulgar
Loc. Moçambique: Madai.
Colector Romualdo Tavares
Data 11-V-1917
Obs. Nº 260

Englerina inaequilatera (ENGL.) S.BALLE
var. Swynnertonii (SPRAGUE) S.BALLE
determinavit S.Balle - 1962

Imp. Moderna, L.da — 8-48 — 10.000 ex.

Figure 14. *Loranthus romualdensis* Pires de Lima. Specimen POV-68985.



69 156

Hibiscus Henriquesii, P. Lima
Palma, 14-8-916
P. Lima
N.º 24

INSTITUTO DE BOTÂNICA «DR. GONÇALO SAMPAIO»
UNIVERSIDADE DO PORTO
N.º geral 69 156
N.º de ordem
Hibiscus Henriquesii P. Lima
Nome vulgar
Loc. Moçambique: arredores de Palma, nos campos incultos.
Colector A. Pires de Lima (dupl. 24)
VIII-1916
—8-48 — 10.000 ex.

Flora Zambesiaca
Hibiscus cannabinus L.
Det. A. W. Exell 1958

Figure 15. *Hibiscus henriquesii* Pires de Lima. Specimen POV-69156.

69212

INSTITUTO DE BOTÂNICA «DR. GONÇALO SAMPAIO»
UNIVERSIDADE DO PORTO

N.º geral 69212
N.º de ordem

Striga diversifolia P. Lima

Nome vulgar
Loc. Mocambique: arredores de Palma, nos campos incultos!
Colector A. Pires de Lima
Data 14-VIII-1916
Obs.

Imp. Moderna, L.da — 8-48 — 10.000 ex.

Figure 16. *Striga diversifolia* Pires de Lima. Specimen POV-69212.

Figure 17. *Polygala limae* Exell. Specimen POV-69000.

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UNIVERSIDADE DO PORTO
N.º geral 69 232
N.º de ordem
Oldenlandia prostrata P. LIMA
Nome vulgar
Loc. Moçambique: arredores de Palma, no mato.
Colector A. Pires de Lima
Data 22-IV-1917
Obs.

Figure 18. *Oldenlandia prostrata* Pires de Lima. Specimen POV-69232.

Exell, *Striga diversifolia* Pires de Lima, and *Tephrosia reptans* var. *microfoliata* (Pires da Lima) Brummitt. However, we found that the type specimen of *Striga diversifolia* Pires de Lima corresponds to the widely distributed *Striga asiatica* (L.) Kuntze.

In conjunction with other recent studies such as those by Darbyshire et al. (2019) and Odorico et al. (2022), this paper contributes significantly to the ongoing efforts to update and enhance the accessibility of data concerning the floristic diversity of Mozambique. We also hope this appraisal of the Mozambique types and endemic taxa in the Pires de Lima plant collection at the Porto Herbarium revives the interest in the African collections present at PO Herbarium.

Acknowledgements

We gratefully acknowledge the anonymous peer reviewers for manuscript feedback.

Authors' contributions

M.B.F (University of Porto) carried out the research, data collection and analysis. C.V. (University of Porto) was the project leader and, as curator of the Pires de Lima collection, supervised the types search and the database of the Pires de Lima collection, and participated in the planning of the work. S.B.V. (University of Lisbon) helped with the historical context of Américo Pires de Lima's mission to Mozambique, the endemism's search and the importance of historical collections for today's biodiversity conservation strategies. J.P. (University of Coimbra) proposed and designed the research, conducted the background research on the species surveys, and analysed and interpreted the data. All authors contributed to writing the paper, discussing the results and commenting on the final versions of the manuscript.

Funding

The funding for the digitisation of the specimens from Mozambique Pires de Lima was made possible by the Portuguese Research Infrastructure of Scientific Collections – POCI-01-0145FEDER-022168 and the IAPT Small Collections Grants (2019–20) 'African Backlog at PO Herbarium: revealing the collectors and specimens of the 20th century in unofficial botanical missions.' The Fundação para a Ciência e a Tecnologia (Portugal) funded Sofia B. Viegas with a PhD grant (2017.128574.BD), providing the necessary conditions for her research work.

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ISSN: (Online) 2311-9284, (Print) 0006-8241

Endangered White-spotted Ketsi Blue butterfly, *Lepidochrysops ketsi leucomacula*, in KwaZulu-Natal

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Dates
Submitted: 5 June 2023
Accepted: 16 December 2023
Published: 8 March 2024

How to cite this article:
Armstrong, A.J. & Ehlers-Smith, Y., 2024, 'Endangered White-spotted Ketsi Blue butterfly, *Lepidochrysops ketsi leucomacula*, in KwaZulu-Natal', *Bothalia* 54, a3. http://dx.doi.org/10.38201/btha.abc.v54.3

The appropriate management of the habitat of the endangered and endemic White-spotted Ketsi Blue butterfly, *Lepidochrysops ketsi leucomacula* Henning & Henning, 1994, is necessary for its survival. Much of the life history and ecology of this butterfly are unknown. The oviposition plant was found to be *Selago tarachodes* Hilliard and the plants that were observed to be visited by *L. k. leucomacula* for nectar all had pink flowers. Monitoring of two populations of *L. k. leucomacula* in protected areas commenced in March 2022. Surveillance and walked transects were the monitoring methods used. Observed threats to this endangered butterfly in protected areas were uncontrolled grazing by domestic livestock and mowing of its grassland habitat. Fencing of its grassland habitat may be a way to control these threats.

Introduction

The future of some South African threatened and endemic butterflies in the Family Lycaenidae, many of which have obligatory relationships with specific host plants and host ants, is precarious (Mecenero et al. 2020). Their populations appear to be in rapid decline towards extinction as evidenced by the relatively steep decline in the Red List Index for the Lycaenidae of conservation concern and for South African butterflies in general (Skowno et al. 2019; Mecenero et al. 2020). The main threats to the South African butterfly taxa of conservation concern are habitat loss and habitat degradation (Mecenero et al. 2020). Degradation of the habitat of threatened butterflies in the Family Lycaenidae can occur in protected areas as well as elsewhere (e.g., Rada et al. 2019) and site-specific management for threatened habitat-specialist lycaenid butterflies may be necessary (Armstrong & Louw 2013; Lu & Samways 2002a,b). Long-term monitoring and surveillance of populations of threatened lycaenid butterflies not monitored previously should be initiated and conducted inside protected areas at least, to detect changes in populations due to habitat degradation or other threats such as climate change and to enable timely conservation interventions (Armstrong & Louw 2013).

Lepidochrysops ketsi leucomacula is endemic to the coastal grasslands of the Pondoland region of South Africa, occurring discontinuously from Margate in the far southeastern part of KwaZulu-Natal to Port St Johns in the far northeastern part of the adjacent Eastern Cape (Van Wyk & Smith 2001; Mecenero et al. 2020; Perera et al. 2021). It is listed as Endangered on the South African Red List of Species (Regional Assessment) owing to habitat loss and degradation through urban and rural residential development and associated fire suppression, agricultural cultivation, subsistence farming, overgrazing by livestock, tourism development and spread of alien plants (Armstrong & Williams 2018; Mecenero et al. 2020). This taxon had not been monitored previously, nor were details of its life history and ecology available apart from its broad habitat type and the genus of its oviposition plant (Mecenero et al. 2020; Williams 2022). The effective management of the habitat of endangered lycaenid butterflies in South Africa relies on the detailed knowledge of the life histories and ecology of the species (Mecenero et al. 2020; Lu & Samways 2002a,b). For example, the vulnerability of the various life-cycle stages of the butterflies and the responses of their host and nectar plants, as well as host ants, to fire season, fire frequency, fire intensity (type of fire) and time of day of burning can be used to formulate management guidelines for each species (Lu & Samways 2002a,b).

Monitoring of *L. k. leucomacula*, the flight period of which is from the beginning of November to the end of April (Mecenero et al. 2020), was initiated in March 2022 in Umtamvuna Nature Reserve at Port Edward and Solomon Gijima Dindikazi Nature Reserve at Margate in KwaZulu-Natal, South Africa. The aim of this short communication is to present novel details of its life history and ecology, which will assist in determining with further research which management actions are appropriate for the conservation of the butterfly and to indicate the threats to this species that occur in the two protected areas.

Materials and methods

Lepidochrysops ketsi leucomacula females that were ovipositing and males and females that were nectaring at flowers or resting on plants were photographed on 8 February 2022 at Umtamvuna Nature Reserve. Four line transects were set up on 30 March 2022 in one region of Umtamvuna Nature Reserve where *L. k. leucomacula* had been observed on the earlier date (Figure 1). The length of each transect is shown in Table 1. The lengths are different owing to the heterogeneity in the areas of suitable habitat in the monitored region of the reserve. The transects were walked along slowly and consecutively by two observers (the authors) together. The number of *L. k. leucomacula* that were observed within 3 m of the transect on one side (for the first two transects immediately adjacent to a grassed vehicle track) and within 3 m on either side of the third and fourth transects (that were not along a track and therefore not disturbed on one side) were recorded. The weather was partly cloudy and warm with a gentle breeze. The transects are intended as permanent transects for future monitoring occasions, except Transect 2, which was discarded because no *L. k. leucomacula* were observed along it on the first monitoring occasion. Monitoring was again conducted on 30 March 2023. Two surveillance visits to the Solomon Gijima Dindikazi Nature Reserve were conducted on 9 February 2022 and 31 March 2022. Owing to the absence of *L. k. leucomacula* at the time of the visits, line transects were not set up there.

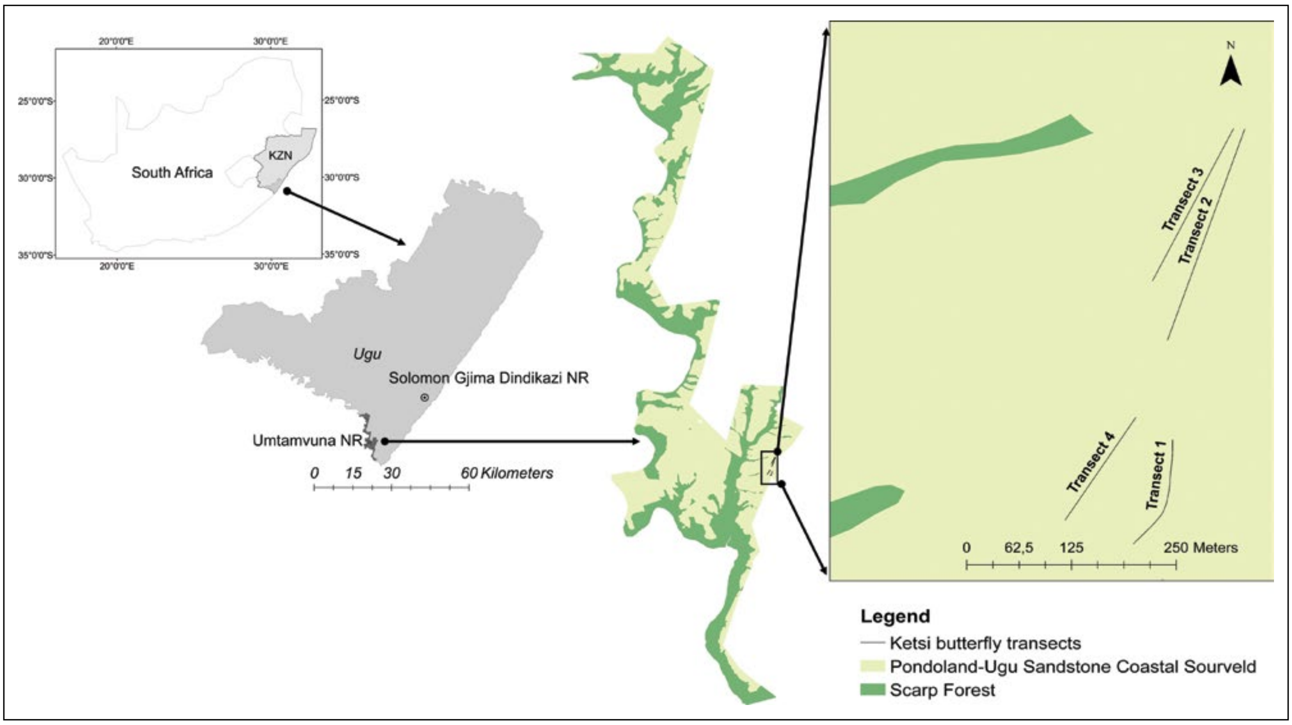

Figure 1. Map of study area, indicating the situation and vegetation types of the Umtamvuna Nature Reserve, KwaZulu-Natal, South Africa, and the relative positions of the four transects (Ketsi transects). Also indicated is the location of the Solomon Gijima Dindikazi Nature Reserve in the Ugu District Municipality. NR = Nature Reserve.

Table 1. Lengths of transects walked and areas searched, numbers of *Lepidochrysops ketsi leucomacula* (*Lkl*) observed, and calculated densities of the butterfly at Umtamvuna Nature Reserve on 30 March 2022

Quantity	**Transect**			
	1	**2**	**3**	**4**
Length (m)	143	275	210	152
Width (m)	3	3	6	6
Area sampled (ha)	0.043	0.083	0.126	0.091
# *Lkl* observed	6	0	6	2
Density (# *Lkl* / ha)	140	0	48	22

Results and discussion

Oviposition hostplant

We recorded *Selago tarachodes* Hilliard as the species of *Selago* utilised by the butterfly for oviposition (Figure 2A–D). This *Selago* species is endemic to the coastal grasslands of the northern Eastern Cape and southern and central parts of KwaZulu-Natal provinces in South Africa (Pooley 1998). Owing to its woody rootstock (Pooley 1998), this plant species likely resprouts after fire, but no information is available for its response to fire season, fire frequency and fire intensity.

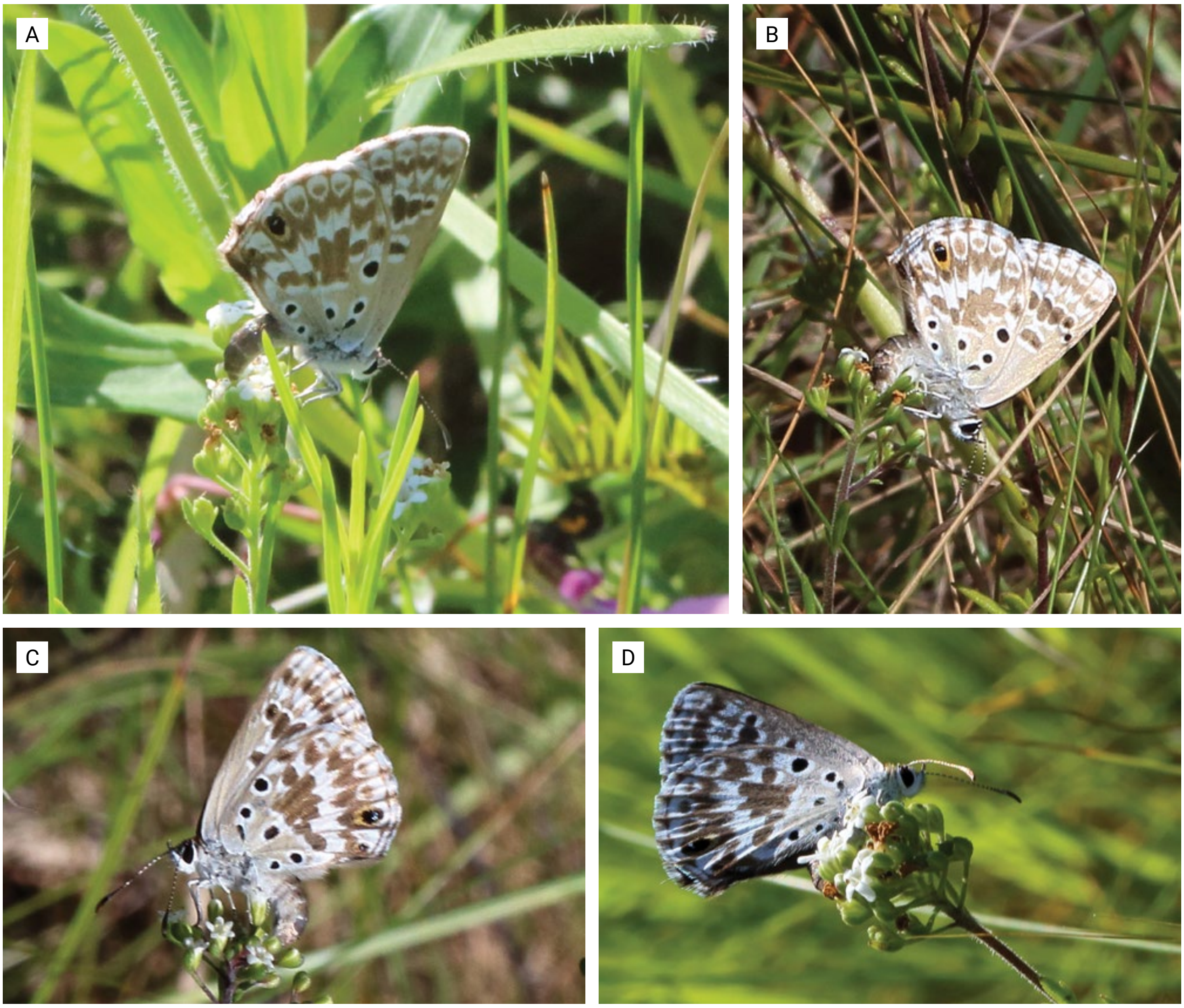

Figure 2. A–D, female White-spotted Ketsi Blue butterflies, *Lepidochrysops ketsi leucomacula*, ovipositing on the hostplant *Selago tarachodes* Hilliard. (Photos by the authors.)

Nectar plants

Lepidochrysops ketsi leucomacula was only observed utilising pink flowers for nectar at Umtamvuna Nature Reserve (Figure 3). Nectar plant species recorded were *Alepidea* sp., *Ophrestia oblongifolia* (E.Mey.) H.M.L.Forbes and *Tephrosia* cf. *grandiflora* (Aiton) Pers. Three pink-flowered *Tephrosia* species were recorded in the area, all of which might be utilised by *L. k. leucomacula* as nectar sources, namely *Tephrosia grandiflora* (Aiton) Pers., *Tephrosia macropoda* (E.May) Harv. and *Tephrosia multijuga* R.G.N.Young. There were other plants flowering at the same time in the habitat of the butterfly that had differently coloured flowers (e.g., Figure 4), but the butterfly was not observed to obtain nectar from any of these plant species. *L. k. leucomacula* therefore seems to be attracted to pink flowers.

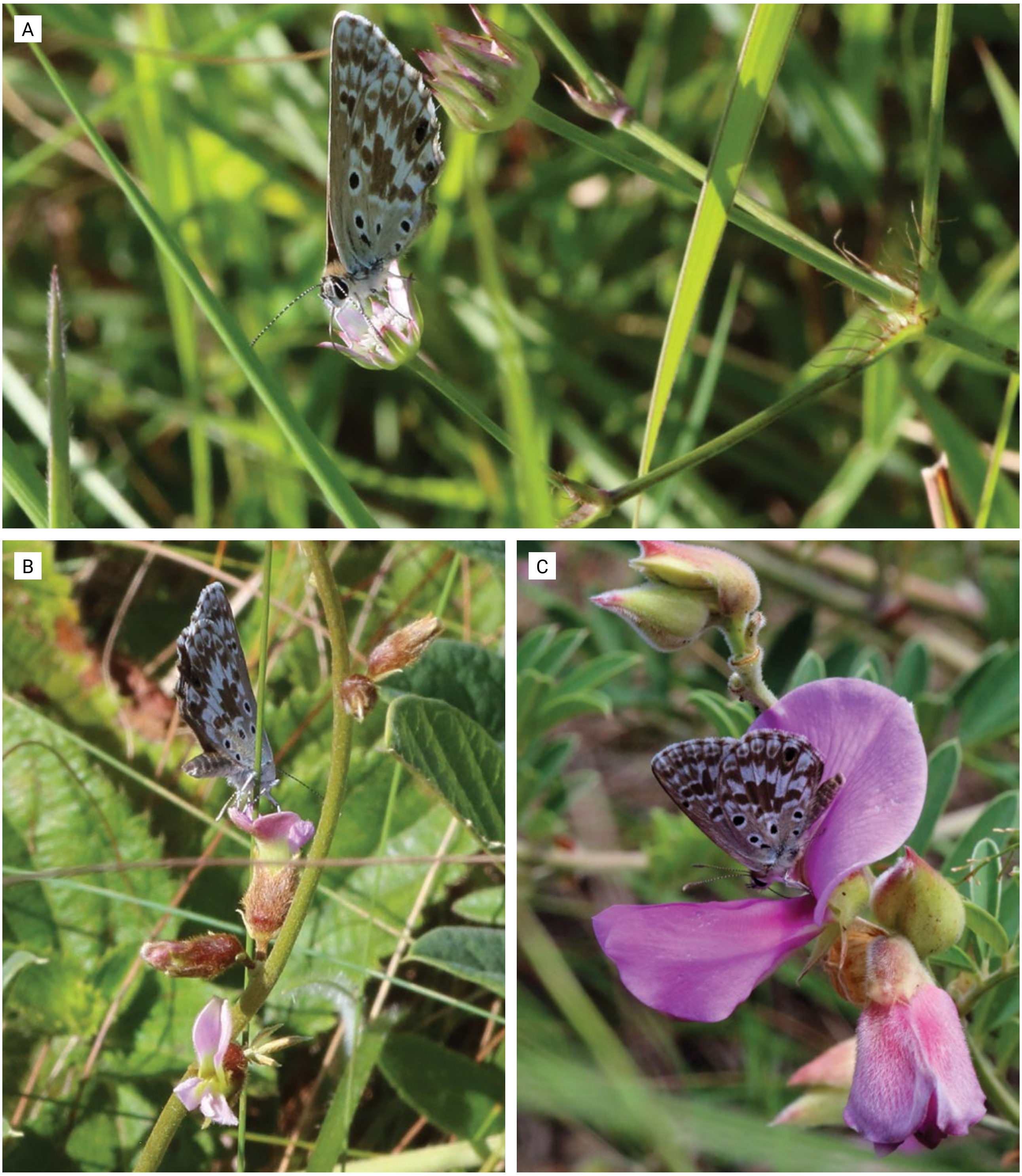

Figure 3. White-spotted Ketsi Blue butterflies, *Lepidochrysops ketsi leucomacula*, nectaring at various plant species with pink flowers. A, *Alepidea* sp.; B, *Ophrestia oblongifolia* (E.Mey.) H.M.L.Forbes; C, *Tephrosia* cf. *grandiflora* (Aiton) Pers. (Photos by the authors.)

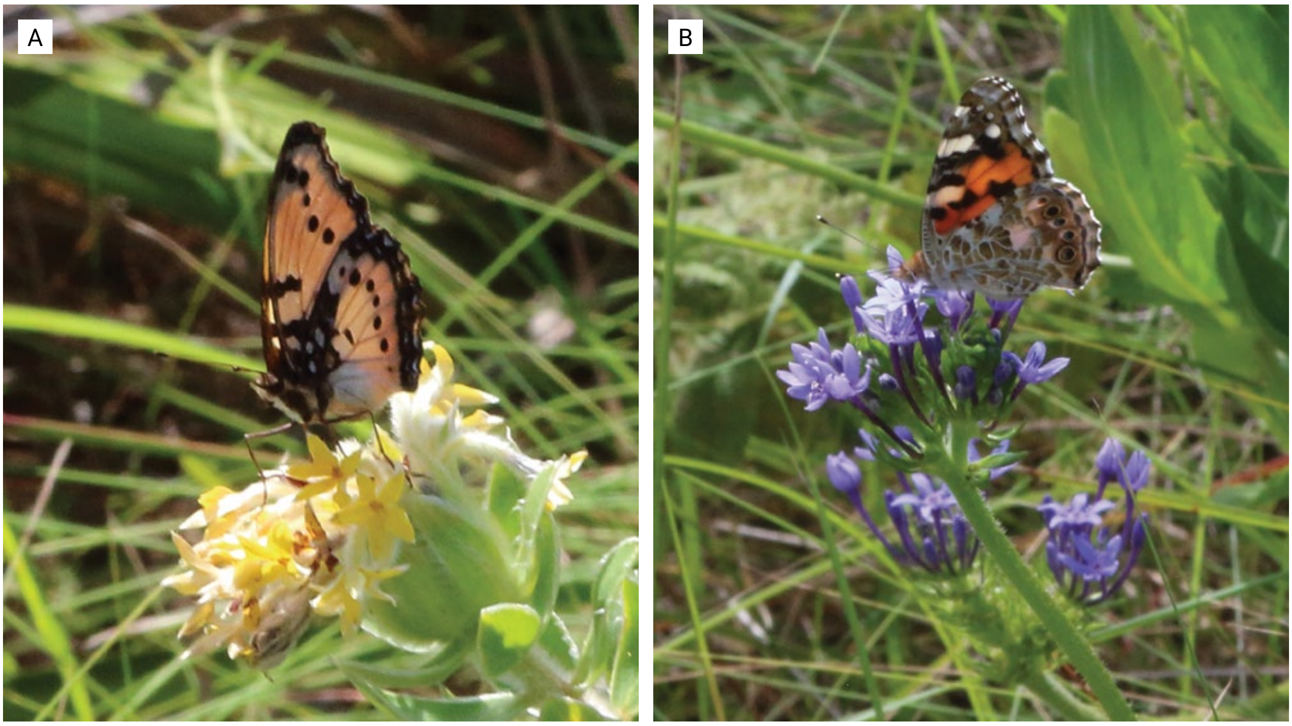

Figure 4. A, Southern Gaudy Commodore, *Precis octavia sesamus* Trimen, 1883, nectaring at *Lasiosiphon anthylloides* (L.f.) Meisn.; and B, Painted Lady, *Vanessa cardui* (Linnaeus, 1758), nectaring at *Pentanisia* sp. on 8 February 2022 in the habitat of *Lepidochrysops ketsi leucomacula* at Umtamvuna Nature Reserve. (Photos by the authors.)

Habitat

Lepidochrysops ketsi leucomacula inhabits primary grassland of the Pondoland-Ugu Sandstone Coastal Sourveld vegetation type in the Umtamvuna Nature Reserve where its oviposition plant occurs. The hostplant is found in relatively small open valleys and the butterfly appears not to fly amongst tall, thick vegetation. This grassland type is critically endangered in KwaZulu-Natal (Jewitt 2018).

Monitoring

The details of the transects and the numbers and calculated densities of *L. k. leucomacula* observed along each are presented in Table 1. Estimated densities of *L. k. leucomacula* varied from 0 to 140/ha. The calculated mean density over the four transects was 41/ha.

The surveillance area was mowed using a tractor in May 2022, an action not aligned with the adopted management plan for the reserve (Figure 5; Ezemvelo KZN Wildlife 2009). Once dried the raked grass cuttings were removed and taken off site. Two observers conducted monitoring using the same methods along Transects 1, 3 and 4 on 30 March 2023, starting at 10:30 when the weather was partly cloudy with a cold gentle breeze. No *L. k. leucomacula* were observed along Transects 1 and 4 (these transects sampled the mown area) and two *L. k. leucomacula* were observed along Transect 3 (in the unmown area). The oviposition hostplant was not observed along the transects in the mown area. Although mowing is a defoliation method, it is not necessarily equivalent to burning. The type of mower used, and the extent and frequency of mowing are factors that require consideration when implementing mowing as a management process in the habitat of threatened myrmecophilous butterflies (Bubová et al. 2015). The compaction of the soil (in which the host ant's nests and the associated *L. k. leucomacula* larvae are assumed to occur) by the tractor mowing the grass, may be detrimental to the conservation of this butterfly species. The tractor tracks were still evident on 30 March 2023. Mowing of the habitat of *L. k. leucomacula* should not be permitted because the loss or degradation of the habitat of an endangered butterfly species should be avoided so that the conservation status of the species does not decline further (Armstrong et al. 2013).

Figure 5. Tractor-mowed portion of the provincially critically endangered Pondoland-Ugu Sandstone Coastal Sourveld at the Endangered *Lepidochrysops ketsi leucomacula* monitoring area in Umtamvuna Nature Reserve in May 2022.

Conservation status of *Lepidochrysops ketsi leucomacula*

The conservation status of *L. k. leucomacula* appears to be deteriorating. One of the reasons appears to be inappropriate management of the butterfly species' habitat in the two protected areas in which the butterfly is known to occur in KwaZulu-Natal. No *L. k. leucomacula* were observed on the two surveillance visits to the Solomon Gijima Dindikazi Nature Reserve. The absence of these endangered butterflies was unexpected because the site is only about 25 km in a straight line from the Umtamvuna Nature Reserve site and the butterfly had been recorded there previously, including on 2 March 2017 by the first author. In fact, the Solomon Gijima Dindikazi Nature Reserve was proclaimed in 2021 to protect two threatened lycaenid butterflies, *L. k. leucomacula* and the Vulnerable Whitish Amakosa Rocksitter, *Durbania amakosa albescens* Quickelberge, 1981 (Mecenero et al. 2020). Various possibilities exist for why we saw no White-spotted Ketsi Blues. One reason could be that livestock have been allowed to graze the grassland and wetland areas (Figure 6). Livestock grazing and trampling of the colony sites are detrimental to the survival of the ant-associated Karkloof Blue butterfly, *Orachrysops ariadne* (Butler, 1898) (Armstrong & Louw 2013) and this may be the case also for the myrmecophilous *L. k. leucomacula*. Livestock

Figure 6. Livestock grazing in the Solomon Gijima Dindikazi Nature Reserve on 9 February 2022.

grazing of the primary grassland and wetlands in the small Solomon Gijima Dindikazi Nature Reserve is largely incompatible with the values for which the reserve was proclaimed.

The area of natural grassland left along the south coast of KwaZulu-Natal is so small that grazing land is not easy to find, and as a result protected areas may be grazed by livestock. The Solomon Gijima Dindikazi Nature Reserve needs to be signposted, and preferably fenced, and the management plan finalised and implemented to prevent the local extinction of *L. k. leucomacula* there. Appropriate protection and management of the butterfly's habitat in protected areas are essential for the continued long-term survival of *L. k. leucomacula* in KwaZulu-Natal.

Conclusions

The grassland habitats of threatened butterflies in protected areas are not immune to impacts caused by defoliation other than by fire at the appropriate intensities and fire return intervals. Where protection from defoliation by livestock or mechanical means (as opposed to fire) cannot be guaranteed by fencing the whole protected area, consideration should be given to fencing areas of grassland habitat required by endangered endemic invertebrate species, particularly those that have relatively small distribution ranges, to prevent their extinction, both locally and globally. Management of the habitat by fire at the appropriate time of year and fire return interval will be necessary. Monitoring of the two populations of *L. k. leucomacula* should continue to assess whether the mowing and grazing by domestic livestock has any long-lasting impacts. We hope that this short note will encourage more research into the life histories and ecology of threatened butterflies in South Africa and to further highlight that even in protected areas in South Africa threats to these butterflies may still operate without appropriate management of their habitats.

Acknowledgements

We thank Graham Grieve for the identification of the nectar plants utilised by *Lepidochrysops ketsi leucomacula*, and Opeyemi Adedoja and two anonymous reviewers for their useful comments on the manuscript. The authors declare that they have no financial or personal relationship(s) that may have inappropriately influenced them in writing this article.

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BOTHALIA – African Biodiversity & Conservation
ISSN: (Online) 2311-9284, (Print) 0006-8241

The mysterious *Widdringtonia wallichii* (Cupressaceae) and the correct scientific name for the Clanwilliam cedar

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Dates
Submitted: 7 March 2023
Accepted: 20 November 2023
Published: 8 March 2024

How to cite this article:
Manning, J.C., Linder, H.P., Govaerts, R. & McNeill, J., 2024, 'The mysterious *Widdringtonia wallichii* (Cupressaceae) and the correct scientific name for the Clanwilliam cedar', *Bothalia* 54, a2. http://dx.doi.org/10.38201/btha.abc.v54.2

We review the complicated nomenclatural history of the Clanwilliam cedar. Much of this centres around the application of the name *Widdringtonia wallichii* Endl. ex Carrière. We are unable to identify any original material of this name and designate a neotype to fix its application as it appears to have been originally intended and as it is currently understood. We also confirm that the correct name for the Clanwilliam cedar is *W. cedarbergensis* J.A.Marsh.

Keywords: Africa, *Frenela hugelii*, *Widdringtonia cedarbergensis*, nomenclature, typification.

Introduction

Widdringtonia Endl. (Cupressaceae) is a small genus of four species of evergreen shrubs or trees of limited distribution in southern and east tropical Africa (Marsh 1966a; Page 1990; Farjon 2005). Among the three southern African species, the Clanwilliam cedar is a large and charismatic tree, and a major focus for conservation efforts.

The Clanwilliam cedar is endemic to the Cederberg in Western Cape, South Africa, and is the only true 'fynbos tree' in a flora of over 9 300 species of seed plants in the Core Cape Floristic Region (Manning & Goldblatt 2012). As such it was important as a source of timber in the region in the past. It is still an icon of the Cederberg Mountain range, a popular hiking and holiday destination that derives its name from the species. The gradual decline in the cedar populations in the region has been well documented, leading to substantial research on the topic, as well as citizen-science activities around replanting the species (Manders et al. 1990; Mustart 1993). The Clanwilliam cedar is a flagship species for conservation and is among the best-researched species in the Cape flora (Richardson 1993). This includes work on palaeoclimates, phytochemistry, conservation biology, population biology and population genetics. There is also a substantial grey literature, published as internal reports by researchers in the Forestry Department, summarised by Richardson (1993).

The taxonomic distinctness of the Clanwilliam cedar has not been in question since specimens were first collected in the middle of the nineteenth century (Endlicher 1847; Masters 1905; Stapf 1933), but its nomenclatural history has been fraught by uncertainties and frequent changes. The species was initially, and for a long time thereafter, known under the misapplied name *W. juniperoides* (L.) Endl. but has subsequently been identified with the name *W. cedarbergensis* J.A.Marsh since that name was published (Marsh 1966b). Recently, however, the older name *W. wallichii* Endl. ex Carrière (Carrière 1867) has been applied to the species, without fully appreciating the identity of this name nor the confusion that this might cause. Although *W. wallichii* was treated as a later synonym of *W. nodiflora* (L.) Powrie by Farjon (2001, 2005), we establish that the application of this name is problematical as it is not possible to identify any original material on which it was based. The attempt by Farjon (2005) to lectotypify the name and thus fix its application is not effective, and we therefore designate a neotype. We also establish that *W. cedarbergensis* is legitimate and that it is the correct name for the Clanwilliam cedar.

Materials and methods

Nomenclatural conclusions are based on the *International Code of Nomenclature* for algae, fungi and plants (Shenzhen Code) (Turland et al. 2018). Authors of plant names are abbreviated following the International Plant Names Index (https://www.ipni.org).

Taxonomic History

The first botanist to collect specimens of the Clanwilliam cedar was Johann Franz Drège (1794–1881), who collected the species in December 1831 near the summit of the 'Blaauwberg' in the northern Cederberg. We have been unable to locate a mountain of this name in the Cederberg but its location 'inter Boschkloof et Honingvalei [Heuningvlei]' places it in the Krakadouw Mountains. Drège distributed his collections under the manuscript name *Callitris arborea* Schrad. (see the duplicate at the Muséum National d'Histoire Naturelle MNHN-P01582404) although others bear the name *Callitris arborea* Lehm. ms. (see the duplicate MNHN-P-P01582405). It appears that Drège also distributed Cederberg material that had been collected at much the same time by C.F. Ecklon & C.L. Zeyher under the same name (see MNHN-P-P01582399).

The name *Callitris arborea* was published without description in the *Zwei Pflanzengeographische Documente* (Drège, 1844: 73 [as *Calitris* (sic.) *arborea*] and on page 170 in the index [as *Callitris arborea* Schrad.]), and the name was also occasionally used in Forestry reports in the late 19th and early 20th centuries. As it was not accompanied by a description it is treated nomenclaturally as a *nomen nudum* and not validly published (ICN *Art. 38.1*: Turland et al. 2018). Diederich von Schlechtendal (1794–1866), Director of the Botanical Gardens at the Martin Luther University of Halle-Wittenberg at the time, proposed the alternative name *Callitris stricta* for the Drège collection (Hooker, 1845; Schlechtendal, 1864) but this is also a *nomen nudum* without description.

Endlicher (1847) subsequently listed and described Drège's collection from the Cederberg under the name *Widdringtonia juniperoides* in his *Synopsis Coniferarum* when he established the genus *Widdringtonia* for the southern African Cupressaceae. His citation of the earlier *Cupressus juniperoides* L. in the synonymy makes it clear that he was publishing the new combination *W. juniperoides* (L.) Endl. based on that name. The name *C. juniperoides* is currently regarded as a synonym of *W. nodiflora* (L.) Powrie, a relatively widespread resprouting species that ranges from the southwestern Western Cape along the eastern escarpment to southern Malawi. Endlicher (1847) was clearly incorrect in applying the name to Drège's Cederberg material. Nevertheless, it was in this sense (i.e., as applying to the Cederberg species) that the name *W. juniperoides* was subsequently used (e.g., Masters 1905; Stapf 1933).

At the same time, Endlicher (1847) listed the name *W. wallichii* as an uncertain species, based solely on a comment by Hooker (1845: 141) about a collection that had been forwarded from South Africa by Nathaniel Wallich. The specimen that Hooker (1845) was referring to is K75280 at Kew, bearing the label '*Pachylepis, P. cupressoides … C. arborea* Schrad., Swellendam, Dr Wallich' (Figure 1).

Although Stapf (1933: 24) in his treatment of the genus for the *Flora Capensis* was aware of the problem of the misapplication of the name *W. juniperoides*, he resorted to the extraordinary and nomenclaturally indefensible solution of excluding all synonyms from *W. juniperoides* sensu Endlicher in order to keep it in the sense that Endlicher (1847) intended. This procedure left the Clanwilliam cedar without a validly published scientific name, and Marsh (1966b) accordingly published the name *W. cedarbergensis* for the species, designating a contemporary collection made by the Forestry expert Hilmar Lückhoff (1916–1995) as the type.

To confuse matters further, although the name *W. wallichii* was published without a description by Endlicher (1847), and is thus a *nomen nudum*, it was mistakenly accepted as validly published in that publication by Farjon (2001, 2005) in his two definitive works on conifers, where it is incorrectly cited as *W. wallichii* Endl.

Here matters rested until Govaerts (2011) realised that the name *W. wallichii* had in fact been validly published by Carrière (1867: 62). This validating description of *W. wallichii* by Carrière (1867) had been noted but ignored by Stapf (1933) in the *Flora Capensis*, and completely overlooked by Marsh (1966a, b) in the *Flora of Southern Africa*. Both authors, however, considered that the name *W. wallichii* applied to the Cederberg taxon (i.e., as synonymous with *W. juniperoides* sensu Engler). The basis for this interpretation appears to be the opinion by Stapf (1933: 24) that the locality 'Swellendam' on the Wallich collection at Kew was an error. This conclusion stems from Stapf's observation that Wallich had annotated other collections of *Widdringtonia* made by him and held in the British Museum as having been collected in the Cederberg. Stapf (1933) did not consider the possibility that Wallich had in fact collected specimens of *Widdringtonia* in both locations!

Farjon (2001, 2005), however, was in no doubt that the Wallich collection from Swellendam was correctly localised and he identified it as *W. nodiflora*. In contrast, Govaerts (2011) followed Stapf (1933) and regarded

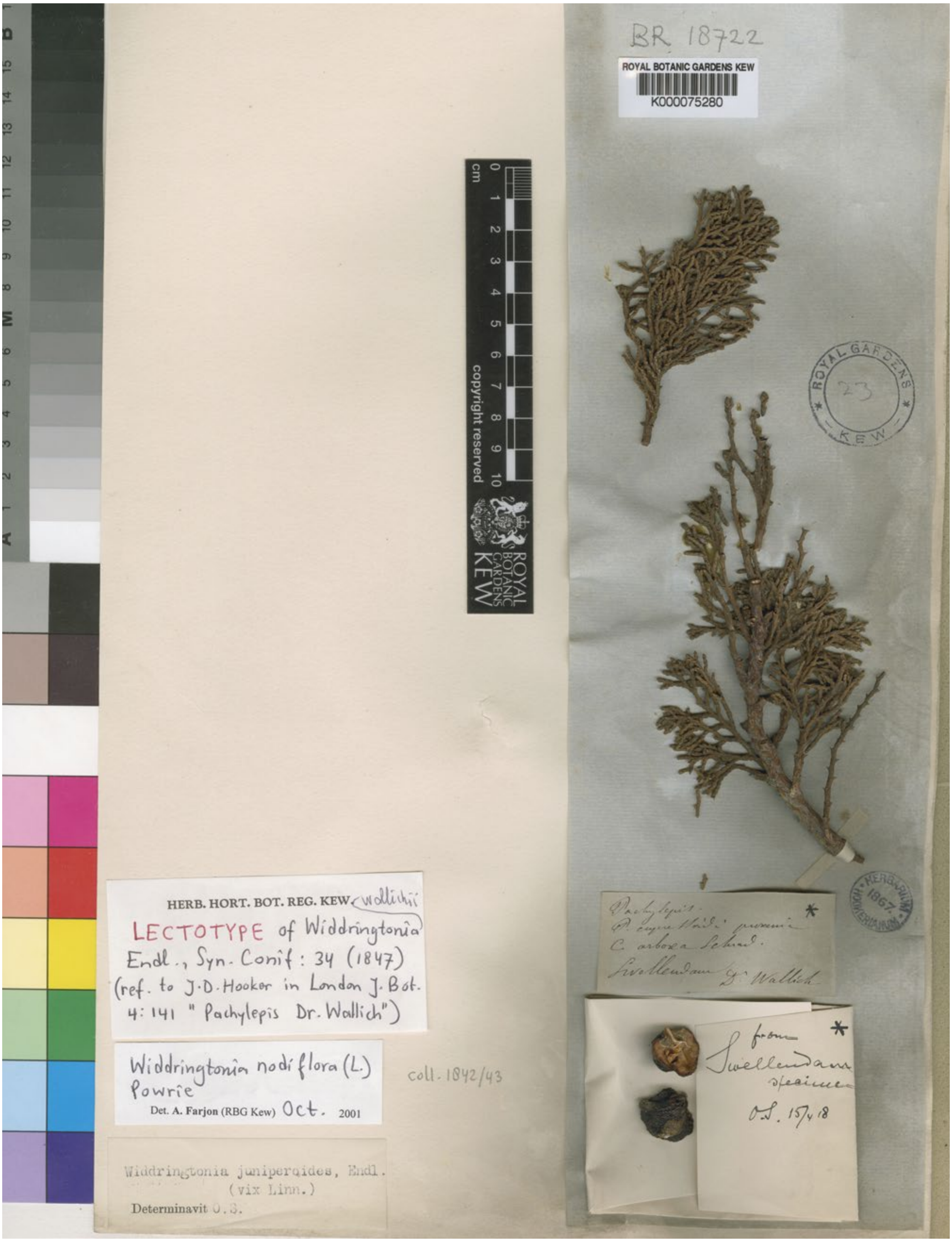

Figure 1. Specimen of *Widdringtonia nodiflora* (K75280) sent by N. Wallich to J.D. Hooker, and the origin of the name *W. wallichii*.

the name *W. wallichii* Engl. ex Carrière (1867) as the earliest available name for the Cederberg taxon, thereby relegating *W. cedarbergensis* to synonymy.

The problem, however, is that it is not clear to which species the name *W. wallichii* should be applied. The protologue (Carrière 1867) contains three elements that could be used to establish the identity of this species: the description, the provenance of the species and the synonym citations. No actual specimen is cited.

The description of *W. wallichii* is very general and deals only with the growth form and the leaves. The female cones and the seeds, which are diagnostic for generic and specific identification (Marsh 1966a), are not mentioned. The description of the height and habit of the species ('arbre pyramidal, atteignnent 12 mètres et plus de hauteur') are evidently based on cultivated plants as this level of detailed information was not generally added to herbarium specimens at the time. It is certainly not on any of the collections of Drège, Ecklon and Zeyher, or Wallich. The location and source of this cultivated material is not given and from the description itself it is not even clear if it was a *Widdringtonia* that Carrière was describing.

The locality data for *W. wallichii* are equally vague, being merely 'Habite l'Afrique australe', with an added note that it was introduced (presumably into cultivation in Europe) around 1844. These observations might be based solely on the information that Endlicher (1847) associated with the name, and do not necessarily indicate Carrière's personal knowledge. Indeed, this vague information contrasts markedly with his detailed entry for *W. juniperoides* (Carrière 1867: 59), viz. '…nommé *Cerdenberg* (sic.), à cause de l'abondance de ces abres, ainis que les montis Blauberg', in which he states it to be not only common in the Cederberg and the origin of the name itself, but critically cites it as occurring on the Blaauwberg, the locality of Drège's collection of the Clanwilliam cedar. This makes it quite clear that Carrière identified Drège's collection with *W. juniperoides* sensu Engler and not with *W. wallichii*.

The synonymy for *W. wallichii* includes three components:

1. 'Frenela Hugelii, Hort., *Carr.* Man. Des Pl. IV. 318. – Tr. gén. Conif. 73 (pro parte). Gord. Pinet. 85 (pro parte).'

   The name *Frenela hugelii* hort. ex Carrière (now a synonym of *Callitris columellaris* F.Muell.) was first published by Carrière (1855: 73) in his *Traité general des Conifères*, based on a plant from Moreton Bay in Australia. The cone is described as having six scales in two whorls, a character state that is found in *Callitris* but never in *Widdringtonia*, which characteristically has four scales in the cone. It is possible that the specimen on which Carrière based his description of *W. wallichii* was previously included in *F. hugelii*, and so the 'pro parte' citation can be understood to mean that it had been incorrectly included under the Australian species. It does not, however, tell us what Carrière (1855) identified as *W. wallichii* but only what he did not.

   The citation by Carrière (1867) of 'pro parte' against the protologue citation of the earlier legitimate name *F. hugelii* Carrière (1855) that he cited in the synonymy of *W. wallichii* is a clear indication that he could be excluding the type of *F. hugelii,* and the name *W. wallichii* should not therefore be treated as an illegitimate superfluous name (ICN *Art. 52. Ex. 5 & Note 1*, Turland et al. 2018). The unqualified citation by Carrière (1855) of the later publication of the name *F. hugelii* in the *Manuel Géneral des Plantes* (Duchartre, 1865) constitutes a later homonym or an isonym depending on typification but does not affect the legitimacy of the name *W. wallichii*.

2. 'Widdringtonia Wallichiana, Gord. *Pinet. Suppl.* 107.'

   (See comments below)

3. 'Widdringtonia Wallichii, Endl. *Syn. Conif.* 34. Lindl. et Gord. *Journ. Hort. Soc.* V. 203. Carr. *Tr. géen. Conif.* 68. Gord. *Pinet.* 335.'

   Widdringtonia wallichii sensu Endlicher (1847) is a name without description and as indicated earlier, is derived from comments that were published by Hooker in an article on the biogeography of the southern conifers, viz. 'Dr Wallich has sent another *Pachylepis* from South Africa certainly distinct from *P. cupressoides*, which may however be the *C. stricta*.' (Hooker, 1845: 141, 142). *Pachylepis cupressoides* is currently a synonym of *W. nodiflora*, and *C. stricta* is a manuscript name that was applied to the Drège collection of the Clanwilliam cedar. Endlicher (1847: 34) evidently did not see the Wallich collection, as he did not provide a description.

Nathaniel Wallich (1786–1854), then superintendent of the Botanical Garden in Calcutta, spent a few years in and around Cape Town on sick leave, and sent his collections to Hooker at Kew. Wallich travelled to the Cederberg with Thomas Maclear in early 1843, and collected seed of the Clanwilliam cedar, which he sent to Hooker (Warner 1989). This is evidently the introduction date of 1844 to which Carrière refers.

The only Wallich *Widdringtonia* collection at Kew is the one from Swellendam in the Langeberg (K75280) that was previously referred to. The specimen includes a female cone and was cited under *W. nodiflora* by Marsh (1966a) and annotated as such in October 2001 by the Kew botanist Aljos Farjon in preparation for his monograph of the family (Farjon 2005). These identifications by two experts in the family are consistent with this locality. Wallich also travelled east of Cape Town in October 1843 with a judge of the Circuit Court (Glen & Germishuizen 2010), during the course of which he would have travelled through Swellendam and thus had opportunity to collect this specimen. From this it seems evident that the *W. wallichii* of Endlicher (1847) refers to the Wallich specimen at Kew and therefore to *W. nodiflora*.

The name *W. wallichii* Endl. (sic.) next appears in the *Catalogue of Coniferous Plants* compiled by John Lindley and George Gordon (Lindley & Gordon 1850), where the name is listed as a 'Doubtful Species' originating from the Cape of Good Hope but without any further information. George Gordon's *The Pinetum* (Gordon, 1858), which was published in several editions, merely repeats the information in Endlicher (1847). In the Supplementum to his work, Gordon (1862) changed the name to *W. wallichiana* but gave no reason for doing this. However, he also added brief descriptive material: 'This kind forms a middle-sized tree, with a stem from 15 to 18 inches in diameter.' We do not consider that this little additional information is adequate to satisfy the requirement for a description or diagnosis and thus to constitute valid publication of the name *W. wallichiana* Gordon. The relevant article in the ICN (Turland et al. 2018) reads as follows: '*Art 38.1.* In order to be validly published, a name of a new taxon (see *Art. 6.9*) must *(a)* be accompanied by a description or diagnosis of the taxon.' The stem diameter information provided by Gordon is clearly not a diagnosis, as defined by the ICN, which reads: '*Art. 38.2.* A diagnosis of a taxon is a statement of that which in the opinion of its definition author distinguishes the taxon from other taxa.' Nor do we consider it adequate as a description. The second edition of *The Pinetum* (Gordon 1875) also includes this descriptive statement. Thus, Gordon's initial treatment (Gordon 1858) was also explicitly based on Endlicher (1847), and so on Hooker (1845) and the Wallich collection at Kew. His later addition of stem diameter (Gordon 1862, 1875) must come from elsewhere.

Although Carrière (1867) attributes the name *W. wallichii* to Endlicher (1847), he could not have actually seen the Wallich specimen at Kew as he neither mentions it nor describes the cones that are preserved on it. We cannot therefore accept the Wallich specimen as part of the original material of the name *W. wallichii* Endl. ex Carrière (1867), based on the relevant article in the ICN (Turland et al. 2018), which reads as follows: '*Art.* 9.4. For the purposes of this Code, original material comprises the following elements: (a) those specimens and illustrations (both unpublished and published prior to publication of the protologue) that the author associated with the taxon, and that were available to the author prior to, or at the time of, preparation of the description, diagnosis, or illustration with analysis validating the name).'

The only undoubtedly original material of *W. wallichii* would thus be the cultivated plant/plants that Carrière described. Farjon (2005: 471), however, sought to designate the Wallich collection at Kew as the lectotype of the name *W. wallichii*. Since he cited the name as being published by Endlicher (1847) and as this is a *nomen nudum*, it cannot have a type and Farjon's proposed lectotypification is therefore not nomenclaturally admissible in any event.

So, what is the original material of *W. wallichii*? Élie-Abel Carrière, (1818–1896) was a French horticulturist at Paris, initially employed as a gardener at the Muséum Nationale d'Histoire Naturelle and soon 'chef de culture' of the living plants until 1869 (Stafleu & Cowan, 1976). We assume that Carrière's quite detailed account of the species in the second edition of his *Traité général des conifères* was based on material, perhaps cultivated, in Paris. We have searched the collections of *Widdringtonia* housed at the Muséum Nationale d'Histoire Naturelle (MNHN-P) but have been unable to locate any material labelled *W. wallichii* that could constitute original material. There are also no published illustrations associated with *Frenela hugelii* that Carrière cites under his *W. wallichii*.

Significantly, *W. nodiflora* was introduced into cultivation in England (under the name *Cupressus juniperoides*) as early as 1756 (Aiton 1789: 373), and there are several cultivated specimens dating from the mid-nineteenth century preserved in the herbarium of the Muséum Nationale d'Histoire Naturelle (MNHN-P) under the names *W. cupressoides* and *W. juniperoides* (e.g., MNHN-P-08602789 and MNHN-P-08602790) that testify to its cultivation in France at the time that Carrière (1867) described *W. wallichii*. Well-grown plants of *W. nodiflora* can also attain a height of 20 m (Farjon, 2005), thus consistent with the height of 12 m or more given for *W. wallichii*.

We are therefore left with two options: either treat the name *W. wallichii* as of uncertain application or designate a neotype to fix its application. As most authors have treated *W. wallichii* as synonymous with *W. nodiflora*, and as the protologue of *W. wallichii* could as readily apply to that taxon as to any other species of *Widdringtonia*, we elect to neotypify the name against a modern collection of that taxon from the same location as Wallich's original sample. This preserves its identity as intended by Farjon (2005) and also retains traditional currency of the name *W. cedarbergensis*. Our proposed neotype, *Marsh 965* (NBG), comprises two sprigs bearing dehisced female cones, and an attached envelope containing mature seeds. A duplicate of this collection lodged at PRE serves as an isoneotype.

There has also been some concern that the name *W. cedarbergensis* is an illegitimate superfluous name for *W. wallichii*. This is based on the inclusion of the name *W. wallichii* Endl., nom. nud. in the synonymy of *W. cedarbergensis* by Marsh (1966b). However, ICN *Art. 46.5* makes it clear that *W. wallichii* is to be attributed to Carrière alone, and so although 'citation of the name itself' (*Art. 52.2(e)*) in the synonymy of a later name does not require citation of the correct place of publication, it does require citation of the name, not of some earlier published 'designation'. As Marsh (1966b) did not cite the valid *W. wallichii* [Endl. ex] Carrière in his synonymy, the name *W. cedarbergensis* is not illegitimate, and thus remains the correct name for the Clanwilliam cedar.

Nomenclature

Widdringtonia wallichii Endl. ex Carrière, Traité Général des Conifères, ed. 2: 62 (1867), syn. nov. pro **Widdringtonia nodiflora** *(L.) Powrie* in J. S. African Bot. 38: 303 (1972). Type: South Africa, Western Cape, '6mi [9.6 km] from Barrydale into Tradouw Pass', 18 Sept. 1968, *J.A.Marsh 965* (NBG, neotype, designated here; PRE-0007375-0, isoneotype).

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BOTHALIA – African Biodiversity & Conservation
ISSN: (Online) 2311-9284, (Print) 0006-8241

Bergbambos tessellata (Poaceae, Bambusoideae) endemic to southern Africa: new record from Limpopo, South Africa

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Dates
Submitted: 30 August 2023
Accepted: 15 January 2024
Published: 8 March 2024

How to cite this article:
Mashau, A.C. & Moshobane, M.C., 2024, '*Bergbambos tessellata* (Poaceae, Bambusoideae) endemic to southern Africa: new record from Limpopo, South Africa', *Bothalia* 54, a4. http://dx.doi.org/10.38201/btha.abc.v54.4

Bergbambos is a temperate C_3 bamboo grass genus, consisting of one species found mainly along southern African mountain ranges (Temperate Afromontane Region). We document here a new record of *Bergbambos tessellata* found in the Thabazimbi area along Hamerkop Street near the fence of an old nursery (non-functional). The specimen was identified at the National Herbarium (PRE) using a light microscope and compared with other herbarium specimens or materials, collected from other South African provinces. This discovery is accompanied by diagnostic features for precise species differentiation, as well as illustrations facilitating visual distinction. Notably, *Bergbambos tessellata* exhibits an unusual geographical range in the Waterberg Biosphere region within the valley. This discovery not only enriches our comprehension of bamboo dispersion dynamics but also engenders a heightened impetus for in-depth investigation into the various factors that underlie its restricted presence within this specific ecological niche. The documentation of this species therefore holds considerable importance in formulating effective conservation strategies and promoting sustainable management practices.

Keywords: *Bergbambos tessellata*, new record, Poaceae, Thabazimbi.

Introduction

Bergbambos Stapleton consists of one species in southern Africa (Soreng et al. 2015). It is a genus of temperate C_3 bamboo grasses, which is mainly found along the southern African Drakensberg (Temperate Afromontane Region). *Bergbambos tessellata* (Nees) Stapleton is the only endemic southern African bamboo that occurs from the Eastern Cape through the KwaZulu-Natal Drakensberg to Lesotho and Free State. The crescent-shaped distribution range of this tree grass is marked in the southwest by the Bamboesberg, west of Tarkastad and in the northeast by Van Reenen's Pass in the Drakensberg. The common name of this grass is *bergbamboes* (an Afrikaans word that translates to 'mountain bamboo'). The *bergbamboes* or mountain grass was firstly described by Nees von Esenbeck in 1841 as a member of the genus *Nastus*, because of similarity of the spikelet with *Nastus borbonicus* J.F.Gmel (for more information, see taxonomic treatment section).

Materials and methods

The *Bergbambos tessellata* specimen was collected in the Thabazimbi area at Hamerkop Street near an old nursery (non-functional) and that specimen was recorded as the first record of this grass in Limpopo, South Africa. The specimen of *Bergbambos tessellata* was identified at the National Herbarium (PRE) using a light microscope and compared with other herbarium specimens or materials, collected from other South African provinces. The conservation of this species in Limpopo is not secured, because it seems like people are unaware of the presence of this plant species in the province. This indicates that the species likely escaped from the old nursery to where it is found today.

Taxonomic treatment

Bergbambos tessellata

Bergbambos tessellata (Nees) Stapleton, in *PhytoKeys* 25: 99 (2013).

Basionyms: *Arundinaria tessellata* (Nees) Munro, in Transactions of the Linnean Society 26 (1): 31 (1868). *Nastus tessellatus* Nees in Florae Africae Australioris Illustrationes Monographicae, Gramineae 1: 463 (1841). *Thamnocalamus tessellatus* (Nees) Soderstrom & R.P.Ellis, in Bothalia 14 (1): 54 (1982).

Type: South Africa, Eastern Cape, 'in monte Katberg, altitude 500', 'without date', *Drege s.n.* (K, K000335516; PRE, lectotype, designated by Soderstrom & Ellis in Bothalia 14 (1): 54 (1982).

Description

Loosely tufted bamboo 1–5 m high; rhizome stout, woody, sympodial with each new rhizome becoming a culm; culm to 20 mm diameter, profusely branched above, dark maroon when young. Leaf blade 50–150 × 8–15 mm, stiff, narrowly lanceolate, tapering to an acuminate apex forming a hard point, strongly cross-veined. Spikelet 16–18 mm long, with tessellate venation; glumes 9.9–15.0 mm long; palea 10.0–12.5 mm long; anthers 7.8–8.0 mm long (Figure 1) (Fish et al. 2015). Flowering infrequently in local populations (flowering recorded in 1908 and 1953) (Soderstrom & Ellis 1982).

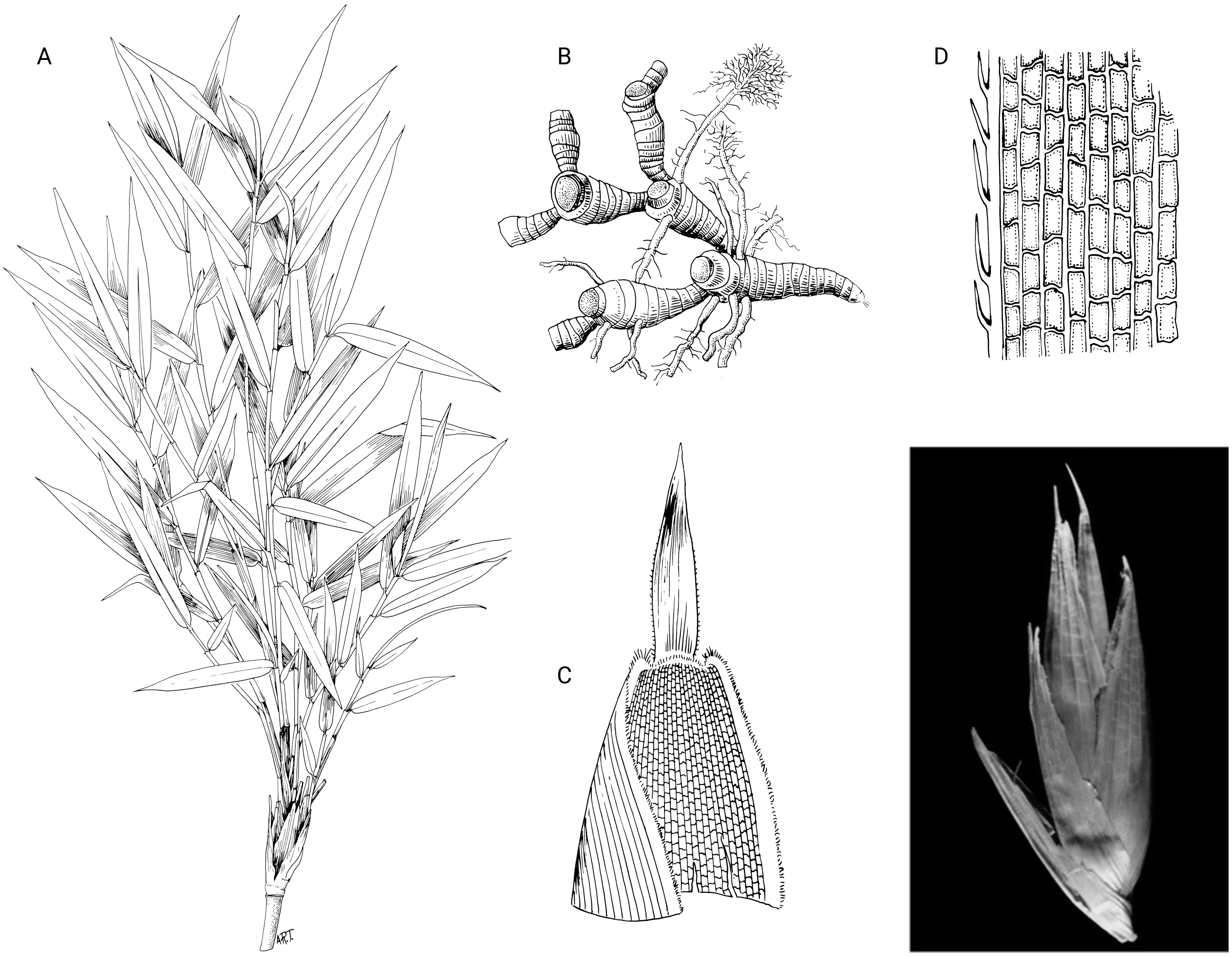

Figure 1. *Bergbambos tessellata*; A, leafy branch; B, rhizome; C, culm leaf (inside view); D, section of leaf blade showing cartilaginous margin and tessellate venation; E, spikelet (16–18 mm). A–D, Artist: A.R. Tangerini, Botany Department, National Museum of Natural History, Smithsonian Institution, USA; E, Photographer: Dr Marinda Koekemoer. Source: Fish et al. (2015).

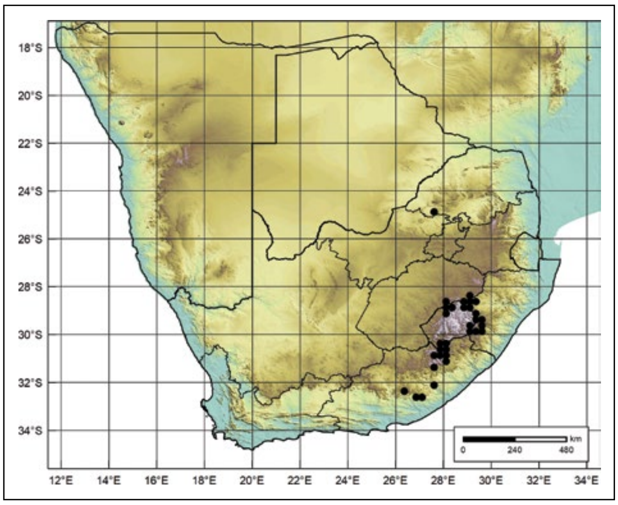

Figure 2. Distribution (●) of *Bergbambos tessellata* in South Africa. Source: map created by Dr Hester M. Steyn.

Distribution and ecology

Bergbambos tessellata is an endemic grass in southern Africa in the Eastern Cape through the KwaZulu-Natal Drakensberg to Lesotho and the Free State (Figure 2). The new record or population of *Bergbambos tessellata* in Limpopo was found in the Thabazimbi area, along Hamerkop Street near the fence of an old and non-functional nursery. The coordinates of the specimen are 24°57′S., 27°40′E (2427DC). This grass is commonly found on mountainsides in wet environments and sheltered ravines, at an altitude range of 1 600–2 700 m a.s.l.

Conservation status and habitat sensitivity

The frequency of *Bergbambos tessellata* in southern Africa is locally common. The identified population is characterised by its limited size, denoting a singular occurrence of this species. *Bergbambos tessellata* displays a distinctive rarity in its geographical distribution, predominantly evident within the Thabazimbi regions of the Waterberg Biosphere. The current investigation documented a range of 100–250 mature individuals within each population surveyed.

Crucially, no indications of local utilisation, which could potentially exert deleterious pressures on the survival of this ecologically significant species, were observed during the course of this study. It is plausible that this species may transition into a threatened status upon thorough examination. Notably, the Thabazimbi area remains largely unexplored, and it is reasonable to conjecture that *Bergbambos tessellata* may exhibit additional occurrences within the broader expanse of the park.

Remarkably safeguarded and endowed with an absence of apparent habitat or population threats, the Thabazimbi region preserves an aura of protection around this species. Nonetheless, notwithstanding human-induced disturbances, harvesting and potential translocations, the intrinsic habitat of *Bergbambos tessellata* faces distinct hazards that plausibly contribute to its enigmatic distribution pattern. Therefore, the meticulous documentation of this species assumes profound importance in understanding its behaviour, habitat and ecological significance within its ecosystem. (Figure 3).

Figure 3. *Bergbambos tessellata*; A, leafy branch; B, tall bamboo grass in foreground. Photographer: Dr M.C. Moshobane.

New collection record

SOUTH AFRICA. **Limpopo:** Thabazimbi area, Hamerkop Street near the fence of old nursery, 2427DC, 16 Mar. 2022, *Moshobane, Mudau & Maema 16* (PRE).

Additional specimens examined

LESOTHO. Basutoland, Leribe, 2828CC, Aug. 1912, *Dieterlen 279, 279A* (PRE); Basutoland, Leribe district, Pitseng, 2928AA, Dec. 1913, *Dieterlen 1010* (PRE); Basutoland, Meniaming Stream, 2928AA, 7 Jan. 1955, *Jact-Guillarmod 2207* (PRE); Bethlehem district, Hlotse Adit. LHDA, 2828CB, 10 Dec. 1991, *Browning 448* (PRE); Upper Quthing River Gorge, after Makoae's, 3027BD, Jun. 1978, *Schmitz 8315* (PRE); southern Basutoland, tributary of Likhaibaning River, 3028AC, 12 Jan. 1946, *Archibald 2750* (PRE); Basutoland, mountain side above Buffalo River waterfall, 3028CA, 14 Mar. 1904, *Galpin 6931* (PRE).

SOUTH AFRICA. **Free State:** Bethlehem, Farm Franshoek, Northeast of Ficksburg, 2828CA, 7 Mar. 1972, *Loxton & Ellis 990* (PRE); Farm Klein Thaba Bosigo 173, 2828CA, 11 Mar. 1972, *Scheepers 1863* (PRE); Fouriesburg, Meiringspoort Resort, 2828CA, 11 Apr. 2002, *Venter 9746* (PRE); Fouriesburg District, about 8 km south of Fouriesburg, Farm Caledonspoort 190, Wynford Family Resort, 2828CA, 3 Nov. 2012, *Bester 11247* (PRE); **KwaZulu-Natal:** Mount aux sources, National Park, 2828BD, 20 Apr. 1919, *Mogg 4221* (PRE); Bergville district, Drakensberg National Park 5 m west of hostel, 2828DB, 18 Apr. 1947, *Codd & Dyer 2778* (PRE); Harrismith, Maweni Heights, north of northwest-facing kloof, 2829AC, 18 Dec. 1963, *Van Zinderen 13* (PRE); Bergville district, Mont aux sources, 2829CB, 28 Aug. 1930, *Hutchinson, Forbe & Verdoorn 54* (PRE); Little Switzerland, top of scree forest by river Bamboo, 2829CB, 15 May 1969, *Anderson 278* (PRE); Bergville district, Cathedral Peak Forestry Station, 2829CC, 25 Mar. 1953, *Killick 1893* (PRE); Estcourt district, Giant's Castle Game Reserve, 2929AB, 1904, *Sim 20517* (PRE); Giant's Castle, 2929AD, Nov. 1914, *Symons 150* (PRE); Underberg, Giant's Castel area, Highmoor Forest Station on little berg, 2929BC, 25 Jan. 1978, *Ellis 3161* (PRE); Underberg, Bushman's Nek, 2929CC, 16 Jan. 1969, *Killick & Vahrmeijer 3976* (PRE); Underberg, Natal, along banks of Umzimkulu River, 2929CD, Mar. 1938, *MacClean 739* (PRE); Underberg, Mkhomazi State Forest, 2929DA, 4 Dec. 1985, *Briggs 11* (PRE); **Eastern Cape:** Drakensburg's, near Barkly East, 2 km west of Danger's Hoek, 3027DB, 18 Dec. 1982, *Phillipson 640* (PRE); Barkly East Division, Faskally, Below Mount Newton, 3027DC, 16 Apr. 1967, *Acocks 23872* (PRE); Barkly East district, Tuschielaw Farm, Maartenshoek, 3027DD, 20 Feb. 1977, *Bigalke 74* (PRE); Maclear, Farm Woodcliffs, Hillside opposite house, 3028CC, 6 Feb. 1992, Abbott 5639 (PRE); Woodcliffs trails, ridge opposite Reed Park, 3028CC, 14 Nov. 1992, *Abbott 5857*; (PRE); Maclear, Farm Fresh Water, 3028CC, 4 Mar. 1992, *Abbott 12180* (PRE); Drakensberg, Maclear, border between farms Pondo Gates and Ben Farraday, QDS: 3128AA, 4 Mar. 1992, *Van Wyk & Abbott 12142* (PRE); Tarkastad, Great Winterberg, east slopes on Farm Winterberg, 3226AD, 15 Jan. 1990, *Linder 5099* (PRE); Victoria East District, Top of Gaika's Kop, Hogsback, 3226DB, 23 Feb. 1942, *Archibald 1* (PRE); Amatole Mountains, Elandsberg, south-facing slope, just below plateau, 3226DB, 28 Oct. 1981, *Phillipson 434* (PRE); Keiskammahoek district, Gxulu mountain, bare plateau on mountain top, 3227BA, 9 Mar. 1948, *Story 3515* (PRE); Victoria East District, Hogsback, 3227CA, *Leemann s.n.* (PRE).

Acknowledgements

Our grateful thanks to: Dr Hester Steyn, National Herbarium, Pretoria, South African National Biodiversity Institute, for the distribution map; the South African National Biodiversity Institute for support.

Competing interests

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

Authors' contributions

A.C.M. (South African National Biodiversity Institute/ University of Witwatersrand) prepared the draft and analysed the data, M.C.M. (South African National Biodiversity Institute/ University of KwaZulu-Natal) collected plant material and made conceptual contributions.

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SANBI
Biodiversity for Life
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BOTHALIA – African Biodiversity & Conservation
ISSN: (Online) 2311-9284, (Print) 0006-8241

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:
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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.

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> 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).

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- 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.
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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).

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  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:

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- 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 num-*

ber (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, 28°43′38.592″S / 31°07′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.

Nomenclatural changes

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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