The classification and mapping of Lapalala Wilderness Reserve, Limpopo

By

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Submitted in partial fulfilment of the requirements for the degree MSc Plant Science
In the Faculty of Natural & Agricultural Sciences
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Pretoria

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February 2021

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Declaration

I, Chevonne Womack declare that the dissertation, which I hereby submit (online) for the degree MSc Plant Science at the University of Pretoria is my own work and has not been submitted by me for a degree at this or any other tertiary institution.

Signature: C. Womack.

Date: 13 February 2022

Abstract

Vegetation classifications and maps form the foundation of understanding spatial variation in vegetation and the environmental conditions driving the occurrence of plant assemblages and form a baseline for detecting changes in vegetation. They are considered an important tool for land-use planning and conservation of natural ecosystems, allowing managers to make informed decisions. The aim of this dissertation was to (1) create a vegetation classification for Lapalala Wilderness Nature Reserve, distinguishing major plant communities and correlated environmental factors, and (2) map the distribution of these plant communities across the study area.

Lapalala Wilderness Nature Reserve spans 48 000 ha and is part of the Waterberg Bioregion in Limpopo, South Africa. The reserve plays an important part in conservation of both flora and fauna, and to support management and develop conservation strategies, the need for an updated vegetation map was recognised. One hundred and eighty 20 x 20 m relevés (comprised of 355 species) were sampled in January-March 2019 for this study. Canopy cover was estimated for all vascular plant species and environmental variables collected in the field include bare ground, rock cover, geographic location and elevation. Slope, aspect, curvature, topographic wetness index, topographic position index, distance to water, number of years since the last fire, and the number of fires in the last 10 years were determined for each relevé. Soil samples were analysed for phosphorus, sodium, calcium, potassium, magnesium, organic carbon and pH, and their particle size distribution was determined.

The OptimClass method identified that the best data-analytical combination for this dataset was Relativized Manhattan dissimilarity index and group average clustering with 10 clusters and no data transformations.The identified communities were Community 1: *Combretum molle-Schmidtia pappophoroides* woodland, Community 2: *Senegalia nigrescens-Heteropogon contortus* woodland, Community 3: *Terminalia sericea-Aristida diffusa* woodland, Community *4: Burkea africana-Eragrostis gummiflua* woodland, Community 5: *Cynodon dactylon-Eragrostis patentipilosa* grassland, Community 6: *Grewia monticola-Vachellia nilotica* woodland, Community 7: *Euclea linearis* shrubland, Community 8: *Cymbopogon pospischilii* grassland, Community 9: *Vitex obovata-Phyllanthus parvulus* shrubland, Community 10: *Andropogon eucomus-Eragrostis heteromera* grassland. Out of the 37 environmentals variables, 21 had a significant effect on the composition of communities, with many of these variables being related to soil texture (n = 10) and soil nutrient content (n = 7).

CART was used to map the communities. However, mapping the study area was not very accurate due to weak relationships between satellite-derived variables and the occurrence of the communities, but estimates a heterogeneous mosaic of communities. Two communities were widely distributed across the study area, Community 1, comprising 66% of the mapped area, and Community 2 (26%), with small patches of Community 3 (3 %) and Community 5 (5 %). An accuracy assessment of the map showed an overall accuracy of 70 % and kappa index of 40%.

In summary, there was no strong differentiation between the communities in terms of species composition or environmental variables, and, as a result, the plant communities do not represent clear management units. Due to a paucity of vegetation studies and landscape-scale vegetation maps in the Waterberg, this study provides an important step in developing a deeper understanding of the vegetation in this ecologically-important region.

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Acknowledgements

I would like to give a huge thanks to Mapula Trust for funding this research. Also, thank you to Lapalala Wilderness Nature Reserve for facilitating this research, especially Hermann Muller and Annemieke Muller, for their assistance and support. I am grateful for this opportunity to have been involved in this study and will remember my time in Lapalala Wilderness Nature Reserve fondly.

To my supervisors, Prof. L.C. le Roux and Prof L. Mucina, thank you. Prof. le Roux, your endless support, leadership and patience throughout this study has been a rock for me and I really appreciate all you have done throughout this research. Your guidance and hard work have elevated this research beyond what I could have done alone. Prof Mucina, your attention to detail and expertise has truly been invaluable to the success of this project.

Further I would like to thank everyone who assisted with this research. Especially Arend de Beer, Bridgette McMillan, Cameron Cullinan, Charne Gouws, Jonathan Womack, Leandri de Kock, Lizo Masters, Megan van den Berg and Steve Mitchell for assisting with data collection in Lapalala Wilderness Nature Reserve, Charl Hertzog, Conner MacKenzie and Mthokozisi Twala for assisting with laboratory work and James Tsakalos for his help during my analyses.

Lastly, thank you to my husband, Jonathan Womack, for his continuous love, encouragement and support over the time of this research, and for all your assistance during fieldwork.

Chapter 1: General Introduction

Savannas are most commonly defined as a plant community comprising a continuous grass layer interspersed with trees, ranging from open grasslands to dense woodlands (Scholes and Archer, 1997; Mucina and Rutherford, 2006; Bond and Parr, 2010). The distribution and structure of savannas are determined by many factors with fire, herbivory, water availability, and soil characteristics (mainly nutrient availability) considered the most important (Murphy and Bowman, 2012; Pellegrini, 2016). Savannas are geographically extensive and are both ecologically and economically important, typically displaying high biodiversity and high endemism (Solbrig et al., 1996). Many important ecosystem services, including food provisioning, water quality improvement and climate regulation are provided by savannas (Galvin and Reid, 2010). The vegetation structure, plant nutritional content and species composition of savannas, along with high productivity, make this vegetation type very suited to grazing livestock and keeping wild game (Scholes and Archer, 1997; Smet and Ward, 2006). Savannas are also favoured for transformation to croplands due to their relatively flat and fertile soils, which can generate good yields and, as a result, high incomes (De Lima et al., 2018). Moreover, livelihoods of many poorer communities are additionally supported by savannas by the provisioning of construction materials and fire fuel (Millennium Ecosystem Assessment, 2005).

Due to the productive nature of savannas, they are subject to strong human utilization and exploitation (Veldman et al., 2015; Aleman et al., 2016). Typically, the agricultural potential of savannas has taken preference over biodiversity, mostly due to the high crop yield and high-quality meat produced in these areas (Bond and Parr, 2010; Veldman et al., 2015). As a result, in spite of its ecological importance, much of savanna vegetation worldwide has been transformed, resulting in large losses of natural vegetation (Foley et al., 2005; Ramankutty et al., 2008). Indeed, future predictions show that cropland and pastureland transformation will be the greatest cause of habitat loss in savannas by 2070 (Aleman et al., 2016).

The transformation of savanna vegetation causes a reduction in species diversity and richness and can alter ecosystem processes and services (De Marco and Coelho, 2004; Ricketts et al., 2008; Wratten et al., 2012; Osborne et al., 2018; Sankaran, 2019). Retaining patches of natural habitats within transformed areas is important for the conservation of species diversity and abundance (Ricketts, 2001). Large conservation programs (such as the Kruger National Park in South Africa or the Serengeti National Park in Tanzania) are vital for maintaining natural vegetation and the associated biodiversity (Joppa et al., 2008; Lucey and Hill, 2012; Beale et al., 2013). However, a considerable proportion of natural vegetation is also conserved in smaller reserves (Holsinger et al., 2019; Maxwell et al., 2020), with sustainable game-farming playing an important role (Tainton, 1999). Proper management of the vegetation in these areas is essential to maintain healthy and productive ecosystems and to preserve ecosystem services (Bruner et al., 2001; Raudsepp-Hearne et al., 2010; Gray et al., 2016; Maxwell et al., 2020), by, for example, maintaining the integrity of the grassy layer and thus the carrying capacity for game and livestock (Tainton, 1999).

Classification and mapping

An objective and repeatable ecological framework is essential to quantify, explain and understand variation in vegetation, which in turn is important for land use planning and conservation. The process of vegetation classification, often called ecological land classification, produces vegetation units (or plant communities) at a specific scale of analysis by grouping vegetation samples with similar species characteristics, identifying areas that could be considered part of the same relatively homogenous unit (Runhaar and de Haes, 1994; Bourgeron et al., 2001; Aho et al., 2008). These plant communities are abstract groupings that delimit (and then name) sections of the vegetation continuum to enable communication and to guide management actions (De Cáceres et al., 2018).

There are three main categories of data collected for a vegetation classification: a) characteristics of the vegetation, b) edaphic and topographic data (e.g., soil characteristics, slope, aspect, debris cover, rock cover etc.), and c) climatic and climate-related data (e.g. water availability and seasonality, temperature etc.; Lambert and Dale, 1964; Werger and Sprangers, 1982). In terms of vegetation characteristics, species composition data are most commonly collected and the majority of classifications currently use only this floristic approach (Werger and Sprangers, 1982). However, data on, e.g., plant physiognomy, plant functional traits and morphology (including growth and life forms, leaf, root, bark, and crown characteristics), phenology and woodiness may also form the basis for classifications (Werger and Sprangers, 1982). Combining both floristic and physiognomic data adds value to the classification, especially for ecologically focused analyses as it gives better insights into adaption and the drivers of the distribution of different vegetation units

(Cain et al., 1956; Beard, 1978; Werger and Sprangers, 1982; Faber-Langendoen et al., 2014).

Vegetation classifications form the foundation of investigating and understanding spatial variation in plant communities, providing insight into the environmental conditions driving the occurrence of different plant assemblages and quantifying vegetation patterning across the landscape. As such, classifications play an important role in conservation (Symstad, 2002; Clegg and O'Connor, 2012). The process of classification, especially the field work component, supplies information on the plant species and communities present within an area and can help to identify populations of rare and threatened species, whilst the final product can aid in identifying threatened, endangered or sensitive habitats (Dias et al., 2004; Hagos and Smit, 2005; Clegg and O'Connor, 2012). Vegetation classifications can also serve as a baseline for future studies, allowing changes in vegetation to be quantified and predicted (Symstad, 2002; Clegg and O'Connor, 2012). Vegetation classifications remain one the most important management tools for natural vegetation, acting as a key input in land-use and conservation planning, and the management of, e.g., restoration actions, burning regimes, and grazing (Bredenkamp et al., 1998; Snyman, 2003; Dias et al., 2004; Skidmore et al., 2010; Holsinger et al., 2019).

There are numerous statistically valid classification tools and data-analytical combinations (i.e. combinations of potential data transformations, resemblance measures, and clustering, or divisive, algorithms) for any dataset, and choosing the most appropriate method for the best results can be somewhat subjective. This may also be problematic, as applying different classification methodologies to the same data sets can show considerable divergences in the results (Aho et al., 2008). However, the best performing method, which will give the most informative and useful final classification, can be identified by running a comparative assessment of all the possible methods for each data set (Lötter et al., 2013). In such a comparison, faithful species provide a valuable internal criterion to identify the most robust classification method for a dataset as they are considered to be good indicators of plant communities (following Lötter et al., 2013). As a result, the statistical methods used, and analytical criteria applied, need to be carefully chosen during vegetation classifications.

A vegetation map simplifies the complex structure of actual vegetation, demarcating the classified plant communities (Bredenkamp et al., 1998). Vegetation maps can be created using models that are applied to a geographic database and assumes that vegetation distribution can be predicted using landscape-scale variables including climate, edaphic factors, geography and topography (Franklin, 1995). However, this relies on the presence of maps (or some other form of spatially explicit datasets) for these variables to already exist or be easy to create. Technological advances in recent years allow for the use of remotely sensed data to be used in the mapping process as well. Hyperspectral data from satellite and aerial imagery has been used to map vegetation with great success and improved access to this data has made mapping easier and cheaper (Padró et al., 2018). However, as remote sensing uses canopy cover and light emittance from the vegetation, it cannot necessarily distinguish units based on floristics (i.e. a botanical classification) and may also fail to detect differences in understory cover and vegetation structure (Mutanga and Skidmore, 2004; Skidmore et al., 2010). Adding topography, climate, edaphic and/or geology data and other features from remotely sensed data (including elevation) to classifications may potentially considerably increase the accuracy of mapping (Zhang, 2014; Woodcock et al., 2002). As vegetation maps are equivalent to a hypothesis of the environmental conditions driving the distribution of vegetation units, accuracy assessments and ground truthing test both the correctness of the map and the hypothesized environment-vegetation relationships (Woodcock et al., 2002).

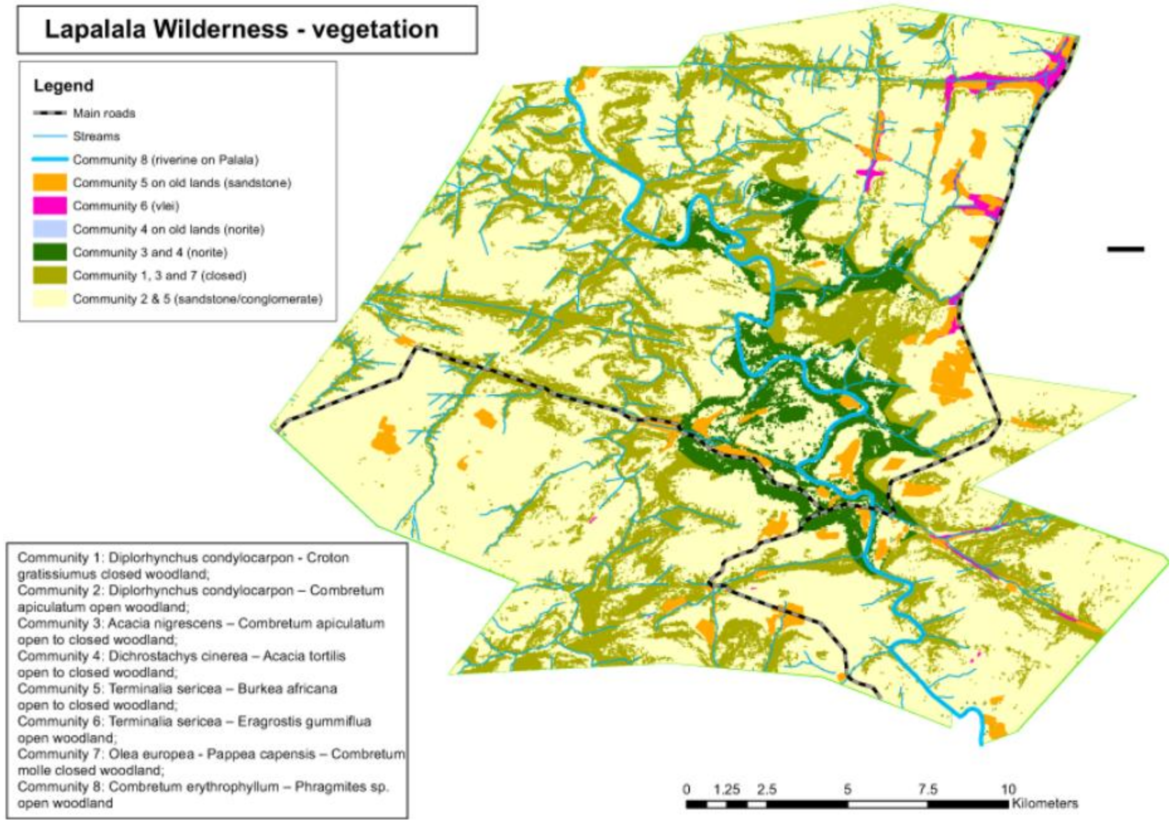
Study site

The Waterberg is a region in northern South Africa that is considered important in terms of biodiversity and conservation (Waterberg District Municipality, 2010; Department of Environmental Affairs, 2012; Desmet et al., 2013). Savanna is the most dominant vegetation type within the Waterberg but there are several other habitats including shaded cliff vegetation and riparian vegetation (Waterberg District Municipality, 2010). The Waterberg Biosphere Reserve was designated by UNESCO (the United Nations Educational, Scientific and Cultural Organization) in 2001 in order to conserve the Waterberg (Desmet et al., 2013). The biosphere reserve aims to balance land management and the use of land for tourism and farming to generate benefits to local communities and conservation. The Waterberg Biosphere Reserve incorporates over 414 000 hectares (1,035,000 acres) and has c. 77 000 people living within its boundaries (Waterberg District Municipality, 2010). A major source of income in the area is tourism, but cattle, crops and wildlife farming are also important (Waterberg District Municipality, 2010).

Lapalala Wilderness Nature Reserve (LWNR) plays an important part in conservation within the region. The reserve was founded in 1981 by Dale Parker and Clive Walker with the aim to conserve both vegetation and wildlife (Lapalala, 2021). LWNR spans 48 000 ha and is situated in the Limpopo province of South Africa. The reserve falls within the Savanna Biome and, in terms of vegetation, forms a part of the Waterberg Bioregion and, more specifically, the Waterberg Mountain bushveld, with a small part of the reserve also comprising Roodeberg Bushveld (Mucina and Rutherford, 2006). The soils of the reserve are nutrient-poor, and are mainly derived from acid sandstone and are part of the Kransberg subgroup (Ruwanza, 2019). Some small patches have more nutrient-rich clay derived by basic norite/epidiorite (Ruwanza, 2019). The reserve falls within areas that have been identified as important within the Limpopo Province for conservation of both terrestrial and aquatic ecosystems (Desmet et al., 2013). This, coupled with the size of the reserve, makes it a valuable place for conservation efforts. LWNR is a sanctuary for both fauna and flora, with minimal human pressures acting on the reserve. Species such as the white and black rhinoceros (*Ceratotherium simum* and *Diceros bicornis*) and roan antelope (*Hippotragus equinus*) are bred in the reserve for conservation purposes (Figure 1). The reserve is largely heterogeneous in terms of topography, comprising large plains, valleys and river systems (Figure 2). One previous vegetation survey, although not extensive and based on woody species only, qualitatively identified eight vegetation units within the reserve (Figure 3; Anonymous, 2014).

Figure 1. Examples of the wildlife conserved in Lapalala Wilderness Nature Reserve, including white rhinoceros with young (top-right; photograph courtesy of Bridgette McMillan), roan antelope (top-left), giraffe with young (bottom-left) and buffalo (bottom right).

Figure 2. Examples of the heterogeneous topography of Lapalala Wilderness Nature Reserve.



Community 1: Diplorhynchus condylocarpon - Croton gratissiumus closed woodland;
Community 2: Diplorhynchus condylocarpon – Combretum apiculatum open woodland;
Community 3: Acacia nigrescens – Combretum apiculatum open to closed woodland;
Community 4: Dichrostachys cinerea – Acacia tortilis open to closed woodland;
Community 5: Terminalia sericea – Burkea africana open to closed woodland;
Community 6: Terminalia sericea – Eragrostis gummiflua open woodland;
Community 7: Olea europea - Pappea capensis – Combretum molle closed woodland;
Community 8: Combretum erythrophyllum – Phragmites sp. open woodland

Figure 3. Previous vegetation classification and vegetation map of Lapalala Wilderness Nature Reserve (Lapalala, 2021).

Aims

The aim of this study was to create a vegetation classification and map of LWNR. This was performed using a field-based vegetation survey to create a vegetation database, which was used in conjunction with environmental variables and satelite imagery to generate a vegetation map (see Figure 4 for the process of creating a vegetation classification and map, from the initial steps of data collection to the final product).

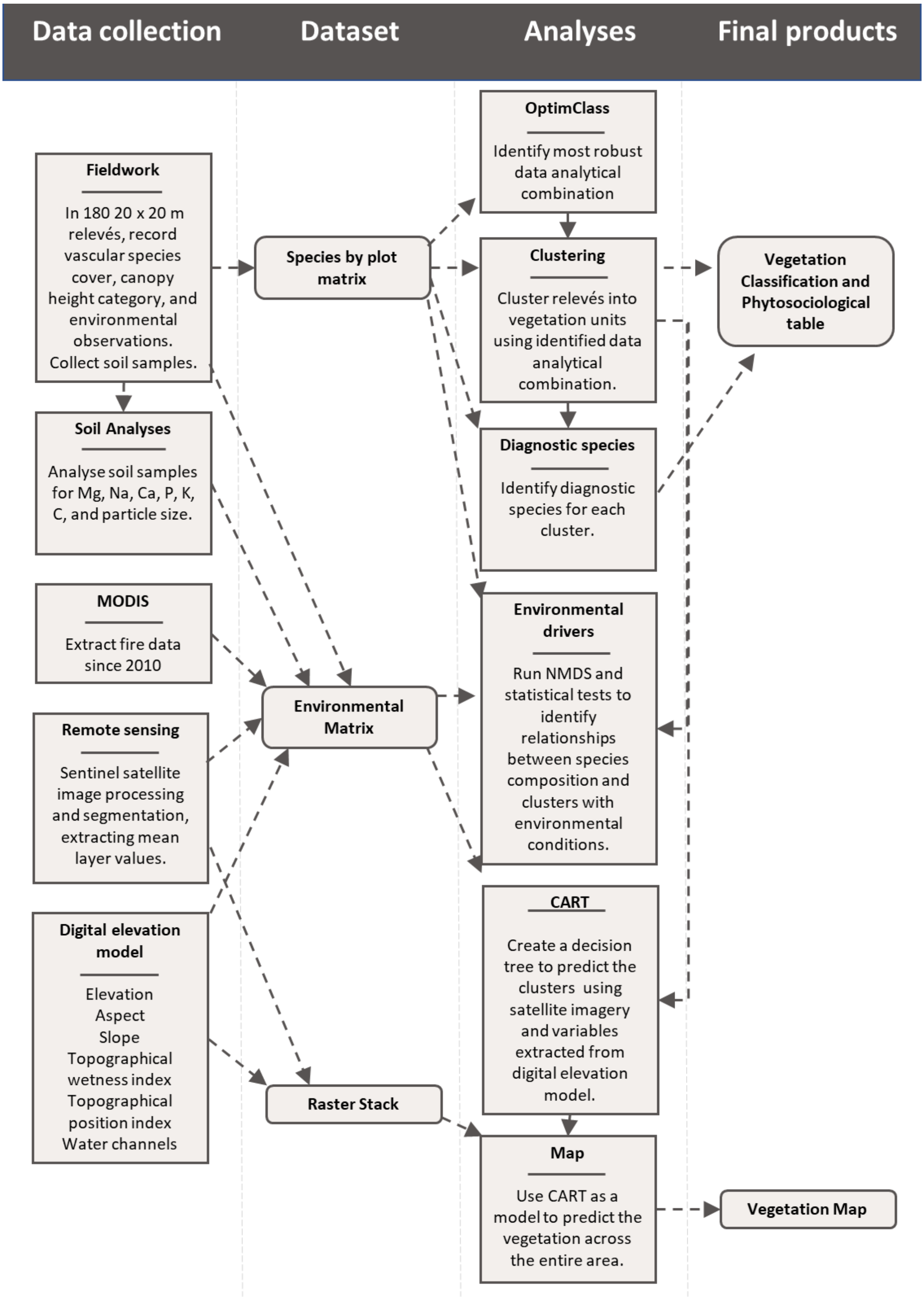


Figure 4. The main steps in a vegetation classification and mapping process. Details for this study are included.

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The Palala River flows through Lapalala Wilderness Nature Reserve (top and bottom).

Chapter 2: The classification and mapping of Lapalala Wilderness Reserve, Limpopo

Introduction

Natural vegetation and biodiversity are decreasing globally, with associated impacts on ecosystem services, sustainable livelihoods, and human health (Millennium Ecosystem Assessment, 2005; Balvanera et al., 2006; Cardinale et al., 2012; Hooper et al., 2012; Tilman et al., 2012; Pecl et al., 2017). The biodiversity decline is driven by anthropogenic impacts, including habitat transformation and climate change (Millennium Ecosystem Assessment, 2005; Johnson et al., 2017; Carwardine et al., 2018; Geary et al., 2019). Formally protected areas and large areas of natural vegetation provide a buffer against these anthropogenic impacts (Bailey et al., 2016). Moreover, reserves and national parks play a principal role in protecting and conserving natural vegetation globally (Holsinger et al., 2019; Maxwell et al., 2020), and proper management of the vegetation within these protected areas is essential to maintain healthy and productive ecosystems and to preserve ecosystem services, both within and beyond conservation areas (Bruner et al., 2001; Gray et al., 2016; Maxwell et al., 2020).

Vegetation classification and mapping are important for informing vegetation management (Dias et al., 2004; Clegg and O'Connor, 2012; Bezuidenhout and Brown, 2021). Vegetation mapping, a form of ecological land classification expressed as a spatial model, defines and maps areas that share similar species composition as plant communities (Bredenkamp et al., 1998; Dias et al., 2004; Mansour et al., 2012). These classifications form the foundation of understanding spatial variation in vegetation, providing insight into the environmental conditions driving the occurrence of different plant assemblages, quantifying vegetation patterning across the landscape, and forming a baseline for detecting future changes in vegetation (Panagos and Reilly, 2006; De Cáceres and Wiser, 2012). Vegetation classifications may be, for example, applied in areas of natural vegetation to identify areas and communities with a high conservation priority in order to guide management actions (Brown and Bredenkamp, 2018). Classification and mapping allow managers to make more informed and effective decisions about practices to manage, conserve and/or protect the vegetation within an area (Bezuidenhout, 2009; Holsinger et al., 2019). A vegetation classification can, therefore, enhance management of a reserve and

act as a tool in land-use planning, conservation and restoration (Bredenkamp et al., 1998; Snyman, 2003; Dias et al., 2004; Bezuidenhout, 2009; Skidmore et al., 2010).
There are numerous valid classification tools and procedures that can be applied during a vegetation classification (Lötter et al., 2013). This includes an assortment of statistical alternatives related to distance (i.e. similarity) measures, data transformations and clustering algorithms (Lötter et al., 2013). However, different combinations of these classification tools can create numerous different divisions in the data, all of which are potentially mathematically correct and ecologically interpretable (as demonstrated by Bruelheide and Chytrý, 2000). It is, therefore, important to have an objective framework to guide the choice of an appropriate and best performing combination of methods, to ensure the most informative final classification (Aho et al., 2008, Tichý et al. 2010).

The vegetation of South Africa exhibits high diversity and endemism (Cowling and Hilton-Taylor, 1994; Mucina and Rutherford, 2006), but many areas of natural and semi-natural vegetation are at high risk of degradation and transformation (Sala, 2000; Rouget, 2003). Indeed, even within formally protected nature reserves rapid changes in vegetation are being observed, presumably in response to anthropogenic environmental impacts, including bush encroachment (Trollope, 1980; Hagos and Smit, 2005; De Lima et al., 2018; Sebitloane et al., 2020) and plant invasions (Rouget et al., 2003; Le Maitre et al., 2004; Stafford et al., 2017; van Wilgen et al., 2020).

The Waterberg region of northern South Africa, located within the savanna areas of the Limpopo Province, is a biologically diverse and topographically heterogeneous area and is important from a conservation and biodiversity perspective (Waterberg District Municipality, 2010; Desmet et al., 2013; Waterberg Biosphere Reserve, 2013; Pool-Stanvliet and Coetzer, 2020). Indeed, in 2012, the Waterberg region was declared a priority area for conservation by the Department of Environmental Affairs (2012). Ecotourism is a major economic income source in the Waterberg, predominantly in the form of game viewing, hunting and recreation in reserves (Waterberg District Municipality, 2010). Lapalala Wilderness Nature Reserve (LWNR) is one of the largest reserves in the Waterberg region (Desmet et al., 2013) and has a strong conservation focus. The reserve falls within an area that has been demarcated as a critical biodiversity area by the Limpopo Department of Economic Development Environment and Tourism (Desmet et al., 2013). In order to more objectively manage the reserve and maintain its conservation goals, LWNR has identified the need for an updated vegetation classification and map.

The aim of this study was, therefore, to classify and map the vegetation of LWNR using a combination of field-based data collection and satellite data. The vegetation classification (1) distinguished the major plant communities within the area, and (2) identified the environmental factors which are correlated with the presence of different plant communities. Further, (3) the classified plant communities were mapped across the study area, providing the basis for (a) a spatially-explicit management tool informing decisions about practices to conserve and protect the vegetation, (b) directing land use planning, and (c) serving as a baseline for future studies, allowing changes in the vegetation to be quantified and predicted.

Methods

Study area

LWNR is situated in the Limpopo Province of South Africa, located 100 km west of Polokwane (Figure 5). LWNR falls within the savanna biome and forms part of the Waterberg Bioregion. Most of the area is classified as Waterberg Mountain Bushveld, with a small part of LWNR considered Roodeberg Bushveld (Mucina and Rutherford, 2006). LWNR comprises c. 48 000 ha of largely untransformed land, with some small areas of previously farmed land. LWNR management has a strong emphasis on conservation and involves active breeding programmes for endangered species such as the roan antelope (*Hippotragus equinus*) and white rhinoceros (*Ceratotherium simum*).

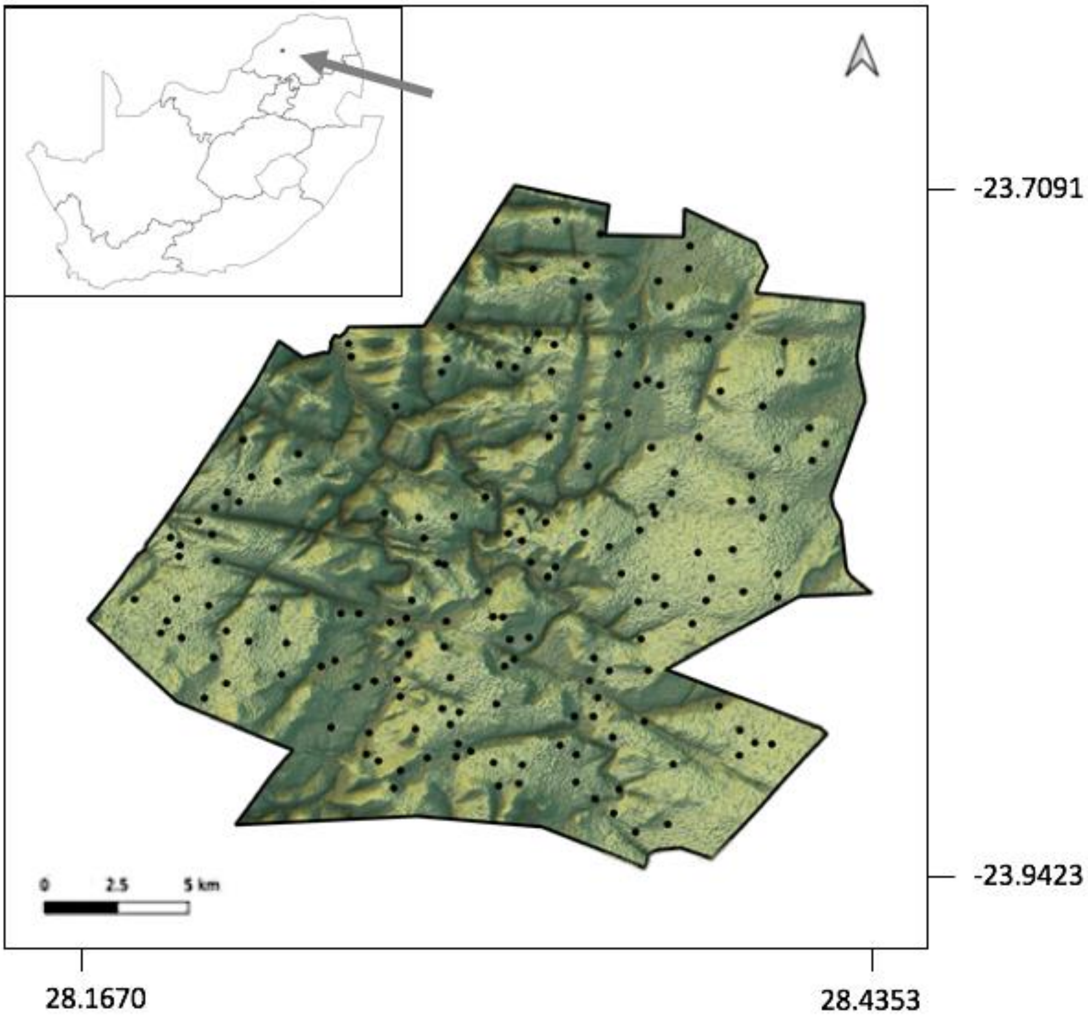


Figure 5. Lapalala Wilderness Nature Reserve, with the inset showing the location of the reserve in South Africa. The sampled relevés are represented by black points. The 3D topography effect was created using the digital elevation model and Rayshader (Morgan-Wall, 2020) package in R.

LWNR is topographically heterogeneous, comprising large plains, valleys and river systems (Figure 6). There are two perennial rivers running through LWNR, the Palala River and the Blokland River, with many smaller streams feeding into these. While there is a lack of published data on the topography of the reserve, analysis of a digital elevation model (DEM; created from ASTER GDEM, a product of METI and NASA, retrieved from USGS/Earth Resources Observation and Science Center; Sioux Falls, South Dakota, https://earthexplorer.usgs.gov; resampled to 20 x 20 m) summarises the main features of the study area. Most of LWNR (c. 60%) is flat or gently sloping (≤ 5° slope), with only c. 2% located on steep slopes (>24°). The terrain in LWNR is fairly equally distributed on different aspects (north-facing slopes = 31%, east-facing = 22%, south-facing = 22%, west-facing = 25%).

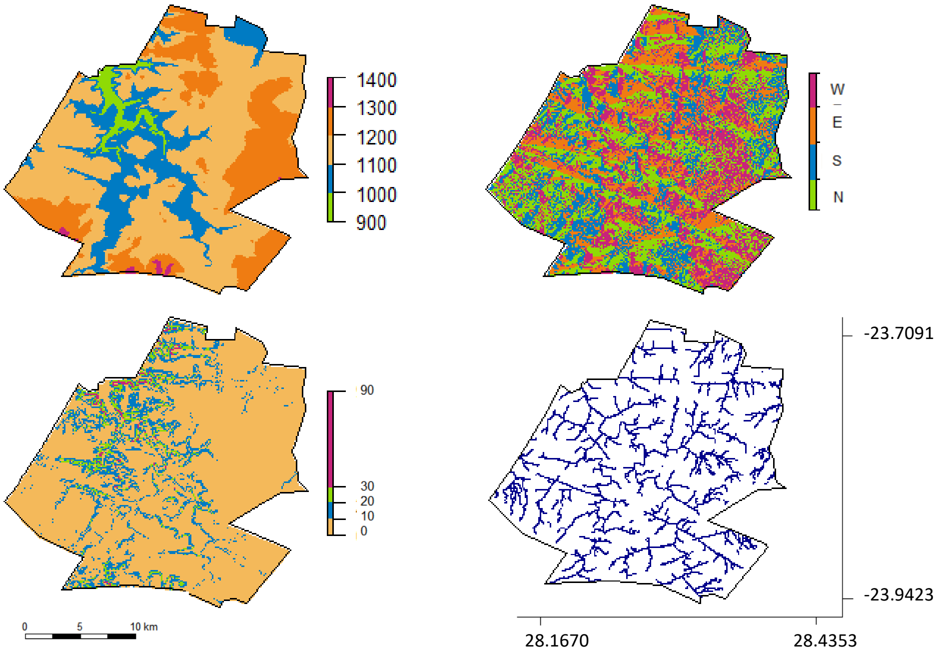


Figure 6. Topographic heterogeneity in Lapalala Wilderness Nature Reserve. (a) elevation (m), (b) aspect (E= east, S = south, W = west and N = north), (c) slope (in degrees), and (d) drainage channels. These maps were derived from a digital elevation model (see text for details).

The mean annual rainfall recorded by LWNR is 546 mm p.a. (Figure 7), although this varies markedly between years (range = 314-942 mm, between 1988 and 2018)**.** There is a strong seasonality to rainfall, with an average spring-summer (September-April) rainfall of 431 mm and an average autumn-winter (March-August) rainfall of 115 mm. LWNR experiences mean daily minimum and maximum temperatures of 20°C and 32°C in the summer, and of 6°C and 25°C in winter (measured within LWNR).

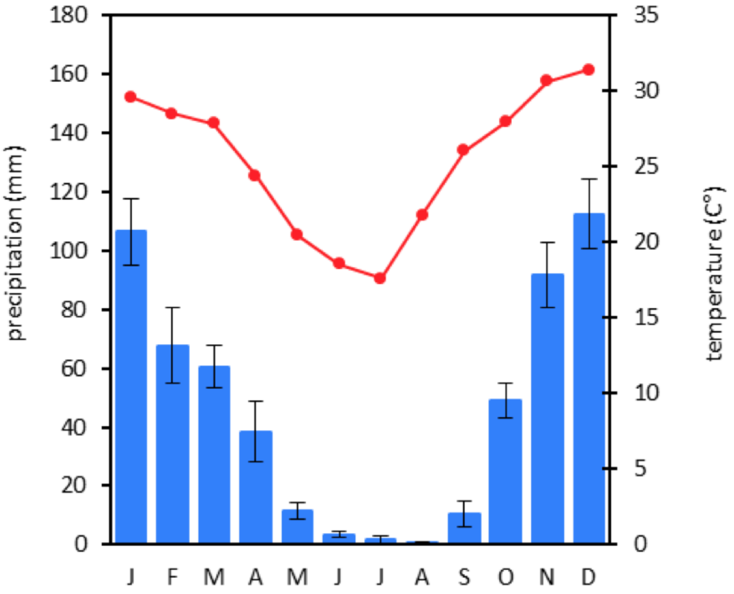


Figure 7. Average monthly rainfall (blue bars; mean ± S.E) and average maximum daily temperature (red line) of Lapalala Wilderness Nature Reserve (1988–2018).

Sampling design

The field sampling was carried out during the peak growing season, starting in mid-summer (January-March) 2019 due to late rainfall that season. One hundred and eighty 20 x 20 m relevés were sampled for the study (see Appendix A for how relevés were laid out in the field). The first 170 relevés were selected using a stratified random sampling design (Mueller-Dombois and Ellenberg, 1974) implemented in ArcGIS (ESRI, 2015). A DEM was used to obtain data on the elevation, aspect and slope for LWNR. These were used in conjunction with a soil map (Dijkshoorn et al., 2008) to stratify LWNR into relatively homogenous habitat units. The relevés were quasi-randomly placed within each stratified area, limiting relevés to not being located within 50 m of strata boundaries (i.e. using a centralized replicate sampling design) to ensure that the relevés are representative of the various strata. An additional 10 relevés were placed in a targeted manner, to capture visibly small-scale or rare plant communities that were missed by the quasi-random placement of relevés. Relevés were not located within 20 m of roads or within 50 m from man-made structures (housing, offices, etc.) as the vegetation in these areas is not necessarily representative of the surrounding natural vegetation (e.g. gardens have been planted with specific, often alien, species). The relevés were also not placed at the bottom of valleys to avoid relevés being located across rivers.

Ten 5 x 5 m relevés were additionally surveyed along the Blokland River and Palala River banks. This vegetation was sampled in an *ad hoc* manner because these habitats pose an elevated risk of encountering dangerous animals. These relevés were smaller than the relevés sampled elsewhere due to the narrow extent of the riparian vegetation away from rivers. The data from these relevés were not included in formal numerical analyses, but were used to informally describe the riparian vegetation in LWNR.

All vascular species rooted within each relevé were identified (including seedlings and saplings) and their percent canopy cover was visually estimated (e.g. Mueller-Dombois and Ellenberg, 1974). Each species' cover was recorded in four canopy layers: herb layer (0-0.5 m), shrub layer (0.5-2 m), sub-canopy layer (2-4 m) and canopy layer (> 4 m). Plant species that could not be identified in the field were identified at the H.G.W.J. Schweickerdt Herbarium at the University of Pretoria.

Bare ground cover and rock cover (i.e. cover of rocks > 10 cm diameter) were visually estimated for each relevé in the field, and the geographic location and elevation of each relevé was determined using a handheld GPS (Garmin eTrex). Using the DEM, slope, aspect (converted to Northness and Eastness following Momberg et al., 2018), curvature, topographic wetness index (TWI), and topographical position index (TPI) were calculated for all relevés. Topographical Wetness Index is a proxy for soil moisture based on topography (specifically the slope and the area of land upslope that contributes to potential water flow), and was calculated using the DEM in SAGA (Version: 7.4.0; Conrad et al., 2015). An estimation of the water channels across LWNR was created alongside the TWI in SAGA, and this was used to estimate the distance each relevé was from a water channel. Topographical position index (TPI) determines the relative position of each pixel of the DEM (i.e. ridge, slope, valley, flat) by comparing the elevation of one point to the mean elevation of neighbouring pixels (resolution 20 x 20 m), and was calculated in SAGA. The curvature estimated for each relevé indicates the relative curvature of the area (i.e. how convex or concave the sampled area is), representing the shape of the land (in contrast to TPI which reflects the relevés' position in the landscape), and was calculated from the DEM in ArcGIS using the 'Curvature' tool. The number of years since the last fire, and the number of fires in the last 20 years, for each relevé was determined using MODIS Collection 6 NRT Hotspot / Active Fire Detections MCD14DL (Justice et al., 2010).

Soil samples were collected from four randomly-selected locations within each relevé. The samples were pooled and air dried prior to analyses. The soil was sieved to identify the size of conglomerates in the soil using 2-, 4-, 6-, and 8-mm sieves. The weight of each size bracket was determined. Soil particles < 2 mm were used for all subsequent analyses. Soil samples were analysed at the University of Pretoria's Soil Laboratory for phosphorus (P), sodium (Na), calcium (Ca), potassium (K) and magnesium (Mg) content using the Mehlich-3 extraction (following Mehlich,1984; Ziadi and Tran, 2008), and pH (KCl; following McLean, 1983). The percentage of organic carbon (C) was determined using the Walkley-Black method (following Walkley, 1935 and Nelson and Sommers, 1983). The particle size distribution was determined using a hydrometer, identifying the percentage of sand (which was further broken down into the five sand fractions) and percentage of clay in each sample (following Bouyoucos, 1962). Silt was calculated as the percentage of soil that is not organic matter, clay or sand (Bouyoucos, 1962).

Vegetation classification

The dataset was stored in Microsoft Excel compatible CSV format and was shared to Lapalala Wilderness Nature Reserve. Since the choice of data-analytical combinations can influence classification results (Tichý et al., 2010), the OptimClass method and faithful species (a species confined to an association) were used to objectively identify the most appropriate and rigorous choices for this study's classification analyses (Tichý et al., 2010; Lengyel et al., 2018; Mucina et al., 2018). The analysis was run using species cover within the four canopy levels in each relevé. Thirty data-analytical combinations (Table S1) were examined in this study (following Lengyel et al., 2018), and were evaluated using OptimClass1 in JUICE version 7.0.102 (Tichý, 2002) to identify and exclude poorly performing combinations (following Lötter et al., 2013). The number of faithful species was determined for each data-analytical combination and for every cluster size ranging from 2 to 50 (i.e. potential number of plant communities). Faithful species were identified with Fisher's Exact Test using fidelity thresholds of $p < 10^{-8}$, $p < 10^{-12}$, $p < 10^{-16}$, and $p < 10^{-20}$ (following Lötter et al., 2013; Lengyel et al., 2018). Each data-analytical combination was ranked using the average performance across all fidelity thresholds. The number of faithful species per number of clusters was then plotted for the top four performing methods (Figure S1). The combination of many faithful species (i.e. a tall peak) and a relatively small number of plant communities (i.e. a small number of clusters) was used to identify the best data-analytical combination and the appropriate number of clusters for the final vegetation classification.

Further statistics were run in R, version 1.1.419 (R Core Team, 2017). Relativized Manhattan dissimilarity index (also know as the Relative Sorenson distance measure) was subsequently calculated in the vegclust package (De Cáceres et al., 2010), and the data was clustered using hclust with group average linkage (UPGMA), using 10 plant communities as the cut-off. Plant Community 1 contained 65 % of the relevés, and this process was repeated to investigate the substructure of this community. OptimClass identified the best data-analytical combination for the analysis of this subset of the data as an absence/presence transformation with Bray-Curtis dissimilarity index and UPGMA average clustering with eight clusters (i.e. eight sub-communities within the Plant Community 1).

IndVal (Dufrêne and Legendre, 1997) was used to identify diagnostic species for each plant community (and each sub-community) using the *labdsv* (Roberts and Roberts, 2016) package. Prominent species for each plant community (i.e. species with a mean cover within the plant community that is higher than the sum of the mean covers of all other plant communities) was determined. Plant communities were named using the diagnostic species, if available, as well as the most prominent species to give more informative plant community names. Finally, dominant species were also determined for each plant community, using the Dominant Candidate Index (DC_i; Avolio et al., 2019) with 0.3 as a cut-off.

A compositional analysis of the vegetation of LWNR was run using a distance-based Redundancy Analysis (db-RDA), with Bray-Curtis dissimilarity (following Tsakalos et al., 2018) using *capscale* function in R and the vegan package. Collinearity between variables was identified vif, using 0.72 as a cut-off value. This removed silt, pH (CaCl), magnesium, aspect, total number of fires, year of last fire, sand (particle size > 250 μm), soil > 8mm, and eastness from the model. An ANOVA analyses (followed by post-hoc Tukey tests, where appropriate) were used to test if environmental variables (Table S2) differed significantly between the plant communities. The Chao Richness Estimator (using *specpool* function in Vegan package; Oksanen et al., 2013) was used to estimate total species richness across the whole reserve and within the five most sampled plant communities (i.e. Community 1-5).

Vegetation mapping

Satellite data was used to map plant communities across LWNR using the image L1C_T35KPP_A010314_20190226T081205, taken on 26/02/2019 with level 1 corrections (Copernicus Sentinel Data 2019, processed by ESA). From this, the red, blue, green and near infrared bands with 10 m resolution, and the three vegetation red edge bands, the second near infrared band and the two short wave infrared bands with 20 m resolution, were clipped to the extent of LWNR and used for analyses. Image segmentation was carried out on the cropped satellite images in eCognition 9.0.1 (Trimble, 2007) with equal image layer weights, a scale parameter of 100, shape of 0.1 and compactness of 0.5. This segmentation was exported as a shapefile, where each object had a mean and standard deviation value for each input layer as well as a mean overall brightness. The shapefile was then rasterised in ArcGIS. The rasterised layers were imported into R and stacked, and the value of all the layers at each relevé position was determined. This satellite imagery data was then added to the environmental data for each of the 180 relevés. A CART analysis (Figure S2) was run using *rpart* (Atkinson and Therneau, 2000) with plant community as the response and the satellite and environmental variables (including the mean and standard deviation of the 10 bands of Sentinel imagery, blue, green, red, NIR, NIR2, RE1, RE2, RE3, SWIR1, SWIR2 as well as brightness, aspect, TPI and TWI*)* as predictors. The resultant decision tree was used to predict the plant community occurring in the rest of LWNR using the rasterised stack and the *predict* function.

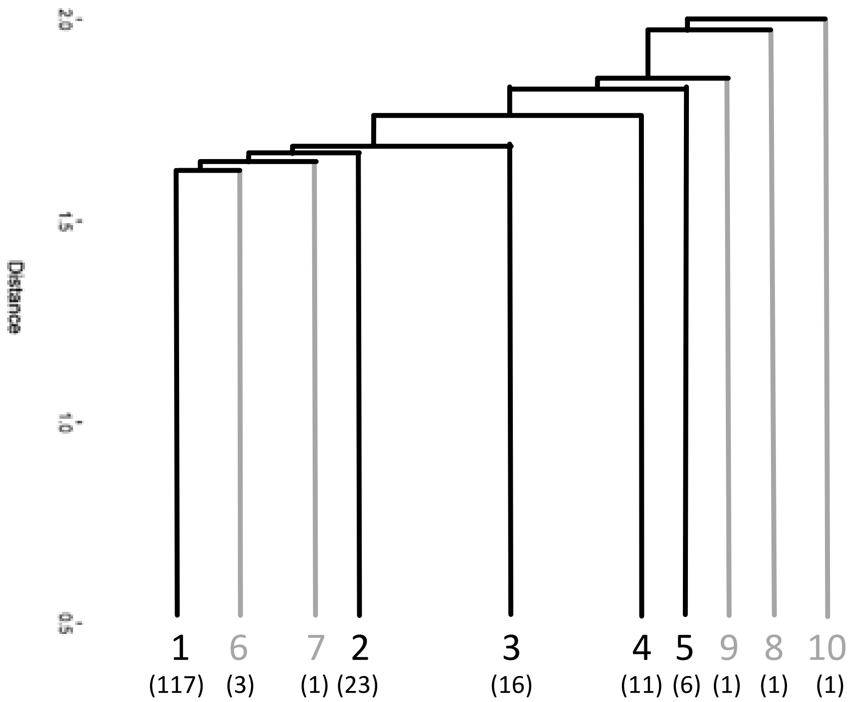
An accuracy assessment was conducted in subsequent growing seasons (January 2020 and April 2021) where 202 points were sampled across LWNR by independent observers**.** Based on diagnostic and prominent species, each sample was classified into a plant community. These points were compared against the predicted plant communities on the vegetation map and the overall accuracy of the map was calculated using the Kappa index (McHugh, 2012).

Results

Vegetation classification

The vascular flora of LWNR was relatively diverse, with 355 species sampled in 180 relevés (see, Table S3 for the list of the 30 most commonly sampled species and Table S4 for the complete list of sampled species). The sampling conducted in this project appears to be incomplete, as the Chao richness estimator predicted a total richness (± SE) of 568 species (± 62). The dominant growth forms in the study area were herbs (193 species), trees (89 species) and grasses (57 species), with shrubs (ten species), succulents (four species) and sedges (two species) being less species rich and having a lower cover. Species richness per relevé averaged 46 ± 14 species (mean ± SD; range 11-86 species). The sampled flora included eight species endemic to South Africa and three invasive species. All species recorded were categorised as being of Least Concern by the IUCN.

The classification process identified 10 plant communities in LWNR (Figure 8; with details in Figure S3). Diagnostic species could only be identified for five of the plant communities (Table 1), but additional dominant and prominent species were identified for all 10 plant communities (Table S5). In the five most sampled communities (Communities 1-5; n = 6 to 117 relevés), the observed species richness ranged from 74-281 species within a community, with 42 species (i.e. 16 %) recorded from all five of these communities (Figure 9). Communities 1 and 2, which were the most thoroughly sampled, had 62 and 33 unique species (i.e. these species were only found in one community) respectively, but had 197 species in common. Less than 10 % of the species recorded in Communities 3, 4 and 5 were unique to these communities.



Community 1: ***Combretum molle-Schmidtia pappophoroides woodland***
Community 2: ***Senegalia nigrescens-Heteropogon contortus woodland***
Community 3: ***Terminalia sericea-Aristida diffusa woodland***
Community 4: ***Burkea africana-Eragrostis gummiflua woodland***
Community 5: ***Cynodon dactylon-Eragrostis patentipilosa grassland***
Community 6: ***Grewia monticola-Vachellia nilotica woodland***
Community 7: ***Euclea linearis shrubland***
Community 8: ***Cymbopogon pospischilii grassland***
Community 9: ***Vitex obovata-Phyllanthus parvulus shrubland***
Community 10: ***Andropogon eucomus-Eragrostis heteromera grassland***

Figure 8. Dendrogram showing the similarity among the 10 plant communities. The communities are numbered in declining order of number of relevés (shown in brackets beneath the community number). The most sampled communities (1 – 5) are shown in black with the communities with three or fewer relevés (6 – 10) are shown in grey. See Figure S3 for the complete dendrogram featuring all relevés.

Table 1. Phytosociological table for the vegetation of Lapalala Wilderness Reserve. The body of the table shows species cover (%) per relevé. Column 2 indicates the community that species are diagnostic for with significance indicated by asterisks, where p < 0.05 (*), p < 0.01 (**) and p < 0.001 (***).

		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		1	2	4	5	6	9	10	11	13	14	15	17	18	19	20	22	25	26	27	28	29	30	31	32	33	34	35	38	39	44	47	48	50	53	54	55	56	58	59	60	63	64	65	66	68	69	70	71	72	73	74	75	76	77	79	81	82	83	84	85	86	87	89	90	91	92	96	99	100	101	102	103	104	105	106	107	108	110	111	113	114	115	116	117	118	120	121	124	126	127	130
Combretum molle	1 ***	17	1	9	5		4	10	7	4	1	1		3	26	2	8	20	22	5	1	7	9	8		1	1	54	7	5	27	1	11	16	1	28	21	10		14	24	8	6	1	17	12	6	4	2	12		14	4				1	14	32		13	5	12	13	14	8	4	22	15	7	11	4	4	18	8	9	3	10	1	8	3	9	23	7	1	13	1	16		10	7	2
Diplorhynchus condylocarpon	1 ***	8		23			19	25	9	6		8		4	4	3		20	17	7		25	13	13	5	2	12	22	18		20	11				9	4		7	14	8	15	15	5	14				1		2	5	10		12			4		9		20	12			19	19		17	9	50	7	14	11		12	18	8		2							5	4	2	26	
Loudetia simplex	1 ***	10	2	12	23	28	2	7		3	11	2	2	1	1	1	2	3	5	5	6	5	1	2	3	2	6	3	3	2	23	14	14	3	5	1	9	6	9		5	3	2		28	1	5	2		2	7	1	10	4	2	1	9	6	9	14	5	8	3	1	1	3	5	1	17	2	1	7	10	1		4	1	2	5	6	22	16	7	2	30	1	2	1			6	15
Schmidtia pappophoroides	1 ***		25	29	2	15	30	4		4	2	1	10	23	1	3	3	2	35	31	27	13	2	8	30	18	32		15	1	7	45	9	11	25	25	3		2	18	15	1	27	2	1	28	7	8	4	16	63	9	13	6	30		15	2	9	25	55	18	38	9	15	12	7	3	8	8	1	6	12	5	22	2		33		4	14			19	1	9	4	8		17	15	6
Elephantorrhiza burkei	1 **			3				1	2	3					6	1	2	3	2	11		4	1	1			2		1		1	3			3	1			3		3	4	1	3		2		1		3	1	2		2				1		2	5	2	2				6		4	9	1	5		10		2	6			1		1	1					1		1		
Harpagophytum procumbens	1 *		1				1							1						1		1		1	1	1	1					1			1					1			1	1		1		1	1	1	2	1			1		1			1			1										1		1									1	1							
Lannea discolor	1 *		1					4	1	4		3		2		1	1	4	7	2		2		6	10	1	1	9	3		1	3	5			2	18		4			1	1		2	1	1	1					1		10	6		1	6	8	10	1	2			1	4			8	1		4	5		2			11		5		1	12			1	1		1	1	
Pseudolachnostylis maprouneifolia	1 *	28						5	8		1							20	1	9	1			1				1	8	4			23	1							1	18				2															1					2	1			18					19									5		1	20			1	10
Pterocarpus rotundifolius	1 *	12	19	5			15	7	3					4	11		8											2		3	20		12	8			4		14	4	9		1	23	3				14		7		9	4				7				7	15		6	14	1	6		17	5		8		21	23		7	4	4			15	25							1	
Xerophyta retinervis	1 *		1	1			2							1					1				4		1		1		1			1	1		2		1					1	1	1				1			3				1			6		1				3					1			1	1									1			3	4		1	1		1
Enneapogon cenchroides	2 ***														1												6					1		1					1																				2	1				1			1									1					1										
Enteropogon macrostachyus	2 ***																																																																																	1										
Ximenia americana	2 ***			2																				3			1					2					5			1											1								1		4	1				1			5					1						4											
Berchemia discolor	2 **													4							1		1																													1																																		1				
Chascanum hederaceum	2 **																															1																																							1																1			
Dombeya rotundifolia	2 **																																										1	1				1																	4		4		5													1					2				
Grewia flava	2 **																					1																																				2															5																		
Heteropogon contortus	2 **					2					1			2						1			1		2		5		1		1	1	1				1	1	1		1			1	2							1	1		1	1				1	1	1					2		9	1			1					1	1	1		1	1					2				
Heteropyxis natalensis	2 **																				1																19					2																												2				8								1										
Panicum deustum	2 **		1	2				1	1					2			1		1					1			1		7														4	1						1		1																					1																1			
Ruellia patula	2 **					1													1					1			1				1																												1									1																							
Senegalia nigrescens	2 **																																																															1																					1				
Ziziphus mucronata	2 **			2				2	1					1	12		6		1					1	1		7				1	7	1		1		1		2				1		4		1					1														2	4	1		1	1				1	1												1				
Chrysopogon serrulatus	2 *						2																						1																														10	2												1																			
Clerodendrum ternatum	2 *			1									1	1												1	1						1																										1													2																		1	
Crabbea angustifolia	2 *				1																							1																																																																
Cymbopogon pospischilii	2 *																																																																																										
Dichrostachys cinerea	2 *	2			1			1	2	1		1	2	1		1			1		1		1	1	5	7	1	3		2	2		6	1	1	1	3	1		2	1			2	1	1	2	1	1	2		2	2			1	1		1	3		4		6	1	4			2	1					21			3	1	1					1	5			1			2
Grewia caffra	2 *	3		5							1	7	2	2	1		2	2	3		1			5	1	1	1	2	2	1	4		7	9		7			11	11		4		2	1		2			1		2	1	2	1	1		1				1	1	4	1	3	1	4		1	1		2		2			1								6	1		2		2	
Grewia monticola	2 *	2	6	2	3		2	2	3	1	3	7	3		3	1		1	1	3	3	1	6	1	2		3	2	1	1	2	2	1		4	16	2	1	4	3	1	1	1	6		3	3	1		1	2	2				1	1		1			2	6			14	4		3			1	4	4	7	3	1	2			4		4	1			6	11		1		1
Gymnosporia buxifolia	2 *																									1													4									7																																											
Lablab purpureus	2 *						1		1								1		1	1				1	1															1												1															1																										
Lantana rugosa	2 *	1		1			1		1		1	1			1	1	2		1						1	1	1		1	1			1			1	1						2		1				1	1	1				1				1		1	1	1		1	2	1	1	1	2					1			1	2	1			1					1	1	1		1
Melhania prostrata	2 *						1	1		1							3	1	1					1			1			1	1		1		1	1	1		1	1	1		1	10		1						1			1			1	1							1	1		1	2			1		1		1	1			1			1	1			1	1		1	
Vachellia tortilis	2 *																																																																																											
Aristida diffusa	3 **		1		2	3	1	1			1		1	1							1				1	1	2		1	1										1			1	1		1	2	1		2		1					1	1								1			1										1						2	7			1	2		9	1
Digitaria eriantha	3 **	10	1	2	1	7	2	8	13		18			2			1	4	2	1	6	1	2	2	6	2	13	4	7	22	11	5	1		6	22	1		4	10	32	2	1	1	1	6	18	11		15	2	2	1		1	1		1		4	3	3	1			4			4	3		1	1	1		1		6		1	1		3	8	17			8	5		9	
Pogonarthria squarrosa	3 **							1																																																																																				
Eragrostis rigidior	3 *	5	1		5	2	1	1				1	1	1		2		2	1						2	1	4		1	1	6			1		2			1	2	5	1		1			7	5				1	2			1					1		1	3	1	4								2	2		1	1	2	2			2		3	1	1	2	1		1	
Euclea natalensis	3 *			1	1			1	1		7				2			1	1		1	1		1				1						1						1					2	1	1			1			1										1			4	1	2	1		2		1		1	1						2						2	1		1	
Fadogia homblei	3 *														1													2																2																																															
Limeum fenestratum	3 *						1	1	1					1							1	1		1					1	1										1	1							1		1		1												1		1								1					1					1	1	1	1					1	
Terminalia sericea	3 *	23			29	2			9		8		1			2		9			42	5		4		1		19						5		4		1			2	11			12				2	1						2	39		9					7	1	1	4	7	1				2						1		2	17	2			6	4				6	4
Cordylostigma virgata	4 ***	1	1			1			1							1															1	1				1	1		1		1									1	1														1	1	1			1											1			1		1	1				1		1	
Eragrostis gummiflua	4 ***	20	1		20	8			9		9		15					1				1						8		24	2					4		7			3	2			7		1									10	5		4				1				1		29						1	1			12	2	2	3	1		1		4	1	1			
Chamaecrista mimosoides	4 **	1	1		1	1	1		1		1	2	1	1					1		1			1	1	1	1	1	1	1	1		1	1	1	1		1		1	1		1		2	1		1		2	1	1	1		1	1	1	1	1								1		1	1			1				1		1		1	1	1	1	1	1		2		1	1	1	1
Helichrysum cerastioides	4 **										1																																																																																		
Indigastrum costatum	4 **	1	1	1	1	1	1	1	1	1	1	1		1	1		1	1	1	1	1			1	1		1	1	1	1	1	1	3					1			1	1	1		1	1	1				1	1			1	1	1	1	1			2	1			1	1		1	2	1	1	1	1							1	1	1					1				1
Sporobolus stapfianus	4 **																																																																																										
Agathisanthemum bojeri	4 *	1			1	2			1		1		1								1	1						4		1	1			1		1	1	1		1	1				1				1							1	1		1				1	1				1	1	1			1			1			3	1	1	2	1	1	6		1	1				
Cyperus esculentus	4 *								4			1	1	1									1					1			1									1		1		1	1	1		1	1	1		1							1			1				1													1														1
Eragrostis racemosa	4 *																																							1						1																				1																	1										
Eriospermum porphyrovalve	4 *																													1						1						1			1			1								1																																						
Faurea saligna	4 *																											3																4											5																																					
Oxalis obliquifolia	4 *																																																						1																											1										
Acanthospermum hispidum	5 ***																																																																																										
Cynodon dactylon	5 ***																																																																																										
Eragrostis patentipilosa	5 ***										1					1																																																																									
Gomphrena celosioides	5 ***																																																														1																							2			
Portulaca quadrifida	5 ***	1						1		1	1					1			1	1					1	1			1			1								1			1						1					1	1												1										1	1	1	1					1				1		6			
Schistostephium crataegifolium	5 ***	3									1	1		1											2		4			1	1	1	1			1				1				2			1	1		2		1			2	2					1					1							1		2		1	1	9				1		1			1	8			
Sida cordifolia	5 ***	2	1						2		1	1	1	1		1	1		1			1	1	1		1		1					2	1			1	1	4			2	1	1	1			1	2			1	1		1	1	1	1	2			1		2	1	1		1		2		1		1	1	2	1		1	3	1		1			1	1	1	1	1		2
Solanum campylacanthum	5 ***	1			1			1	1		1	1	1	1	1	1	1		1	1	1			1	3		1	1	1			1	1			1	1	1	2			1	1	3		1	1			1	1	1	1		3	1				1	1	1		2	1	1	1			1			1		1	1		1	1	1	1		1		1		1	1	1			1
Boerhavia repens	5 **																																																																																										
Cleome monophylla	5 **																			1				1	1								1							1				1		1		1				1												1		1								1					1											1		1	
Dicerocaryum eriocarpum	5 **																																																																																1										
Sporobolus festivus	5 **											1																	1												1																																			1				1		10				1	2			
Tribulus terrestris	5 **																																																																																									
Alternanthera pungens	5 *																																																																																									
Bulbostylis hispidula	5 *		1										1	6								1		1		1			1			1								1						1		1		4		1						1						8														1	1					1		1							
Datura ferox	5 *																																																																																									
Gardenia volkensii	5 *				1	1				1	1	1			1						1					3				2									1						1		1					1				1			1				2					2	1		1					1				1					1							
Gisekia africana	5 *	1	1				1	1	1		1			1			1		1		1			1	1	1	1		1		1	1	1		1	1				1	1	1				1		1		1	1	1	1		1											1						1		1				1						1	1			1			1	1
Hirpicium bechuanense	5 *																																																																																									
Melinis nerviglumis	5 *																																																																																									
Monsonia angustifolia	5 *					1			1					1							1				1			1	1	1		1							1	1									1	1	1								1				1		1							1		1				1	1									1		1	1
Oxygonum sinuatum	5 *																																																																																									
Satureja biflora	5 *										1																																																																														
Seddera capensis	5 *																																1														1																																											
Tragus berteronianus	5 *					1			1		1	1	1	1												1	1		2	1						1				1			2	2		1	4	3		1		3										1				1									2			1		1				1	1			1	2		1	
Urochloa panicoides	5 *							1		1					4			3	1	1							1		1		1	1			1						1		1			1	1				1	1						1			1		1						1		1						1	1						1				1				
Waltheria indica	5 *	1	1		1	1	1	1	1	1	1	1	1		1		1	1	1		1		1	1	1	1	1	2	1	2	1	1		1	1	1			1	1	2				1	1	1	1		1		1			1	1			1	1			1	1		1		1	1	1		1	1		1		1	1		1		1			2		1	1	1	1		

Table 1. Continued.

		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5
		131	132	133	135	136	137	138	139	142	147	148	150	154	155	157	158	159	161	163	169	170	172	173	176	177	180	3	7	16	24	36	41	61	62	78	93	94	95	97	109	119	122	128	129	140	146	156	160	164	166	171	175	8	40	43	46	49	98	141	143	144	145	162	174	178	179	12	42	45	52	57	80	112	134	149	165	168	21	51	88	123	125	151
Combretum molle	1 ***	14	2	4	15		21	5	7	6	1	2	8	2	10		1		10	1	10		13	1		14		7		20	5		1	12	5				2					1	6									1	1		1											5		1	6				10	1							
Diplorhynchus condylocarpon	1 ***	17	7	9	31		1	12	5	11		8	17	19	16	7	1	16		7		39	14			8				61				4											44			2											1													1										
Loudetia simplex	1 ***	28	7			1		3	3	1		2	4	2	19	7	30	11	1		15	7		19	17	13	1				1		2				2								2								1														2			8				5							3	
Schmidtia pappophoroides	1 ***	4	1	3	4	1	32	15	4	52	24	15	4	6	6	6		12	14	11	3	5	9	1	20	9		3		1					8						1			1	2		2	3																																	
Elephantorrhiza burkei	1 **	1			10	1		2	3	2		1	12	2	1	2				3	1	1	7			4				1	1			1	1						1				1								1						1											1												
Harpagophytum procumbens	1 *	1									1			1	1								1		1																			1																																						
Lannea discolor	1 *	11	3		1		1	2	1	9			3	2		2	1	12	1		1			4		6		2		19						1							6											1													7			1												
Pseudolachnostylis maprouneifolia	1 *	2	1				3	10	10			14	12	18	8	29	1	12					19							2	1			1	5				2												1																					1											
Pterocarpus rotundifolius	1 *	26		8	3		48	3	29	6	1		2	21	1	5	2	33	13	10		16			22	13			2			1		14				8	5				22		3	7		11	2				18																																
Xerophyta retinervis	1 *						1					1			1					1				1		1											1																																																	
Enneapogon cenchroides	2 ***			1		1			1	2										8								2				1		1	54	3	1			1	4	10	1			13	2			1	23	17																														
Enteropogon macrostachyus	2 ***																2					1	1				1					12	1	1	4		1		1						1	1	3	2	13		8	2																															
Ximenia americana	2 ***													1								2			1			7	2						3	1	1		3		1	1	1	1	1		3	3	10				1																														
Berchemia discolor	2 **														4		1											1			1			1	2	1	1		4					9	2		4				2							1																									
Chascanum hederaceum	2 **																																1				1				1	1	1		1		1		1	1		1	1							1																								
Dombeya rotundifolia	2 **									2														1				11	1	12	21	1		8			2	4	1				2	6	1		3				2	6		1						2																							
Grewia flava	2 **																										2		3			2			2	6	1	3	8		1	2				15	5		8	1						1	1			1																								
Heteropogon contortus	2 **	1	13			1			3	2	1	1			2	1	1	1		2	1	1	1	5	1	3		6	2	7		43	1		2	2	23	5		1	9	1	1	9	10	1		8				18	20		1														1			2	2		1				1						
Heteropyxis natalensis	2 **	2															3			1							1	2			2					4	12	3	3				2	5	1				8	1	1																																	
Panicum deustum	2 **	1		1												1						1	1						7				5		1			4					1		4	9		9	14	2	12	1																																	
Ruellia patula	2 **								1	1												1						1							1						1	1	1		1			2				1																																
Senegalia nigrescens	2 **																																1		1	18			1			1		11	1	24	1		49	1	29	13									1																			1					
Ziziphus mucronata	2 **	2				3		1	6	1	1			6		1		3				6			1		143	2	2	16	13	1	6	4	6	1		1	5	1	1		12	4	2	1	1	9			6									5			2	1	1															1					
Chrysopogon serrulatus	2 *		1		1																3											8		2								14		1			1				1																																
Clerodendrum ternatum	2 *																	1									26						1			1						3	1		1	1						1																																
Crabbea angustifolia	2 *																					1								1						1							1									1	1																															
Cymbopogon pospischilii	2 *																																							1			3	1	1		1		1					2						1																												
Dichrostachys cinerea	2 *	2	1	1	1			1	1							1	1		1	1		6	1	4	8			13	27	3	34	65	14		4	19	2	10	6	75		2	4	5	3	22	13	3	35	1	3	12	2	1	1	14	2		15	33		19	1	2	2	2	4	3	1		2	1		1				1	1	1	4	1	1	1
Grewia caffra	2 *	5		2		33	1	1			1	9		6	1	3	1	2		3		5	3	1	2	1		7	8	2	16	6	4	30	2	7			15	11		1		1	1	15	1	4	26		23		1	4			1		1	1		11	2	3			1	1	2			2					1						
Grewia monticola	2 *	3		1	1	2	3	1	1			1	2		1	2	2	3	1		1	2	3		3			5	2			1		10	1	10		17		1	2	1	3	2	1	11	3	3	26	2	16	2			1					5	1	3			1	1		1							1			2		1	10	1		
Gymnosporia buxifolia	2 *																												2	1						2								2								1																																
Lablab purpureus	2 *							1																									1							1		1		1	1		1		1		1				1							1																		
Lantana rugosa	2 *	1			1			1									1				1			2				1	1	1	3	3	1	3	1	1	1	2	1		1	1	3	2	2	1	1	1	1	1	1	2	3						1	1	1				7	1												1		1	1				1
Melhania prostrata	2 *	1		1	1	3	1		1					1	1	1		1		1		1	1		1	1	3	1	1		1	1	1	1	1	1	1	1	1		1	1		1	1	1	1	1	1	1		1																											2		1		1		
Vachellia tortilis	2 *																												2				22							5	15	39	13					4			1																											1						18		
Aristida diffusa	3 **	1	14								1	5	3		1		1				5			2				1		1						2							2	1		1			1			1	2	1	1	4		1	1		11	1	2		1	7	15	1				1						1			1			
Digitaria eriantha	3 **	1	6		9	1	1	1	7	8	1		2	1	1	3		1		8	21	7			16	9		1		8		3	2	2	1		1	3		2			12	1	5	13	1	6				6	24	22	2	19	19	5	3	5	48	14	26	1	30	27	45	1	4			1				3	1	2	2	14	2		23	1
Pogonarthria squarrosa	3 **																																	1																						1		1				1			3	3																	
Eragrostis rigidior	3 *			1	1	1	1	1	1									1	1		1							1	1		1	3		2	1		1	3		1	11			1	1	1		1	1	1		5	3	5	1	3	2		3	4		6	8	2	1	11	7				5		10	3			2	1			1		3	
Euclea natalensis	3 *			1		2						1				1						1		1				1		1	1			1	1	1			1	1			1	1	1		1				3				2		2	1	1	2			1	2			1	1				1												
Fadogia homblei	3 *																															1																								4			8						3																			
Limeum fenestratum	3 *						1																					1																										1		1					1	1	1																				
Terminalia sericea	3 *		1												2		10			2	2		2							19	6			12						12	1		1											2	33	23	35	8	2	14	1	100	55	7	3		53	15	5	3	6	31	5	6		6	15	1	35		19			1
Cordylostigma virgata	4 ***			1	1		1				1					1			1		1									1								1								1							1		1									1			1	1		3			1	1	1	1	1						
Eragrostis gummiflua	4 ***																4				8					3								4																					1	4	1	1				17				2			48	65	28	12	33	54	7	10	24	65	80						
Chamaecrista mimosoides	4 **	1				1	1				1				1		1				1			1	1				1	1				1				1			1		1										1	1	1			1			1	1	1		1		1	1	1	1	1	1		1	1		1	1	1					1
Helichrysum cerastioides	4 **																																																																														1						1										
Indigastrum costatum	4 **	1	1	1	1	1	1	1	1			1	1	1	1	1	1	1		1	1	1	1	1		2				1				1	1										1				1						1	1		1					1				1	1		1	1	1	1	1	1	1	1								1
Sporobolus stapfianus	4 **																																																																																				9	1								
Agathisanthemum bojeri	4 *										1						1				2			1					2				1													1						1	1	5	2				1				7		2	4	1		1	1		1	1		1	5		1	1			
Cyperus esculentus	4 *											1				1																	1																					1	3																1			1		1		3								
Eragrostis racemosa	4 *																1							1		1									1																																											1	2	1	1			1					
Eriospermum porphyrovalve	4 *																																																								1																	1		1				1							
Faurea saligna	4 *																																																																																			1	7								
Oxalis obliquifolia	4 *																													1									1																																										1				1				1							
Acanthospermum hispidum	5 ***																																																																																													1					2
Cynodon dactylon	5 ***																											1														1																7	5	2							11										1					50	75	30	30	48	32
Eragrostis patentipilosa	5 ***																											1															7														1							1		1						1										12	5	3	4		2
Gomphrena celosioides	5 ***																															1										1																											1	1									1							1	1	1			1
Portulaca quadrifida	5 ***			1												1				1														1						1								1											1				1				1													2	1	1	1	1	1
Schistostephium crataegifolium	5 ***			1							1												1		2	1			2							3		2			15	1	1		1	1		1	1	3	1	4	7	1				1		1			1				1									1		2	9	1	3	1	1	15
Sida cordifolia	5 ***	1		24		1	1					1	1		1	1							1		1			1	1		5			1	1		1	1	1		1	1		1	1				1	1	2			1		1		2	1	1		1	1	5	1	1	1		1	1	1			1	1	1	1	1	1	1	1	1	1	4
Solanum campylacanthum	5 ***			1	1	1	1	1			1	1	1	1		1		2		1		1	1		1	1			1	1	1		1	1	1	1	1	1		1	4	1	1	1	1	1	1	1	1	1		1	1			1				1			2	1		1	1	1	1		1					1		1	1	1	1	2	3	2
Boerhavia repens	5 **																																							1																																												1			1		
Cleome monophylla	5 **																																					1										1									1						1	1							1								1			1		1
Dicerocaryum eriocarpum	5 **																																																									1			1		1							1			1								1			1	1
Sporobolus festivus	5 **	1		3							1						1									1																																					1									1	1						3								1	1	1	
Tribulus terrestris	5 **																										1																																																																	1	2		
Alternanthera pungens	5 *																																																																																																3		
Bulbostylis hispidula	5 *											1				1																																											10																								3		1		3		6	
Datura ferox	5 *																																																																																												1					
Gardenia volkensii	5 *		3				1				1						7		1		1	1		2	15						2	1								2					2											1					1	1						1		2			1	1				1	1		1	1			1	1
Gisekia africana	5 *				1							1	1		1														1									1	1						1			1								1		1				1	1																	1		1	1
Hirpicium bechuanense	5 *																																																																																																		1	
Melinis nerviglumis	5 *																																																																																																		1	
Monsonia angustifolia	5 *		1								1	1								1					1									1		1								1			1	1						1		1		1				1							1									1				1	4
Oxygonum sinuatum	5 *																																																																																																3			
Satureja biflora	5 *						1																				30													1																			1		1	1				1										1				1	
Seddera capensis	5 *																																																																																																		1	
Tragus berteronianus	5 *			1							1																2	2								1	3			2	18	1	1	1	1			1	6		8	3	1		3		1	1			1	7														1	12		27			2
Urochloa panicoides	5 *				1				1				4															1									1		1	2					2			1	3							1				1																					1		1			1
Waltheria indica	5 *	1		1	1	1	1		1			1	1	1	1		1				1		1	1	1	1	2	1	1	1	3		1	1	1	1		1		1	1	1	1	1	1	1	1		1		2	1	1		1	1	2		1	1	1		1		1	1	1	1	1			1	1		1			3	1	2	1		2	1

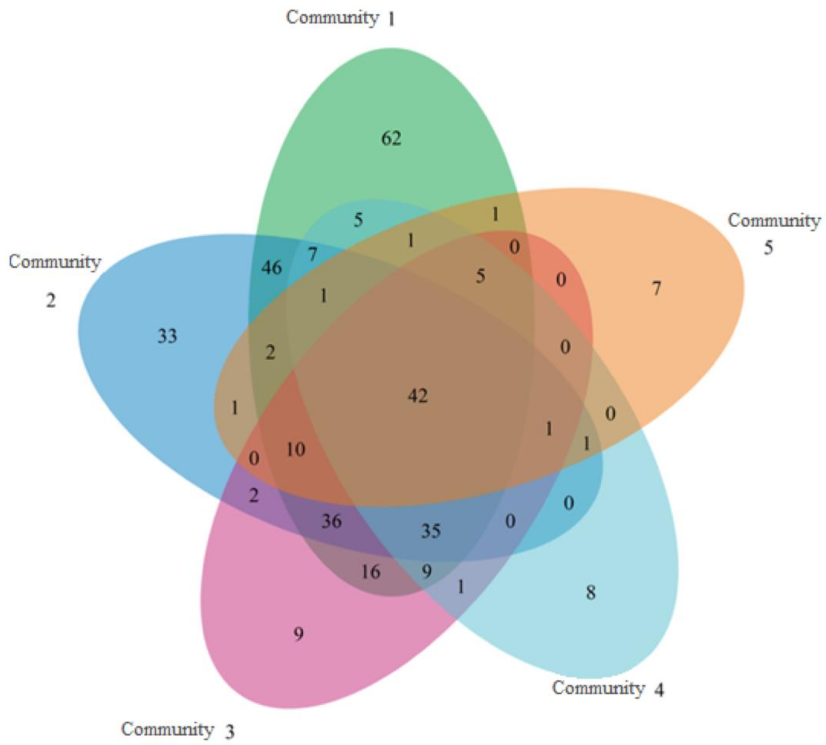


Figure 9. Venn diagram showing species richness in the five most sampled communities of Lapalala Wilderness Nature Reserve, with the richness of species occurring in multiple communities indicated in overlapping areas. For example, 42 species occurred in all five of the well-sampled communities and 46 species occurred in Communities 1 and 2 only.

The three growth forms with the highest cover across all the communities were grasses, herbs and trees (Figure 10). Looking at the five most sampled plant communities, on average, Community 2 had the highest tree cover (c. 100%, although this ranged from 10-200) and Community 5 had the highest grass cover (range 35-96 %, mean 66 %), while herb cover was relatively similar across all the communities. Sedges and succulents had very low cover and were found in few communities (Figure S5). The vegetation in Communities 1-4 had similar canopy structures (Figure 11), but Community 5 had low cover between 0.5-4 m and a higher herb layer cover than the other communities.

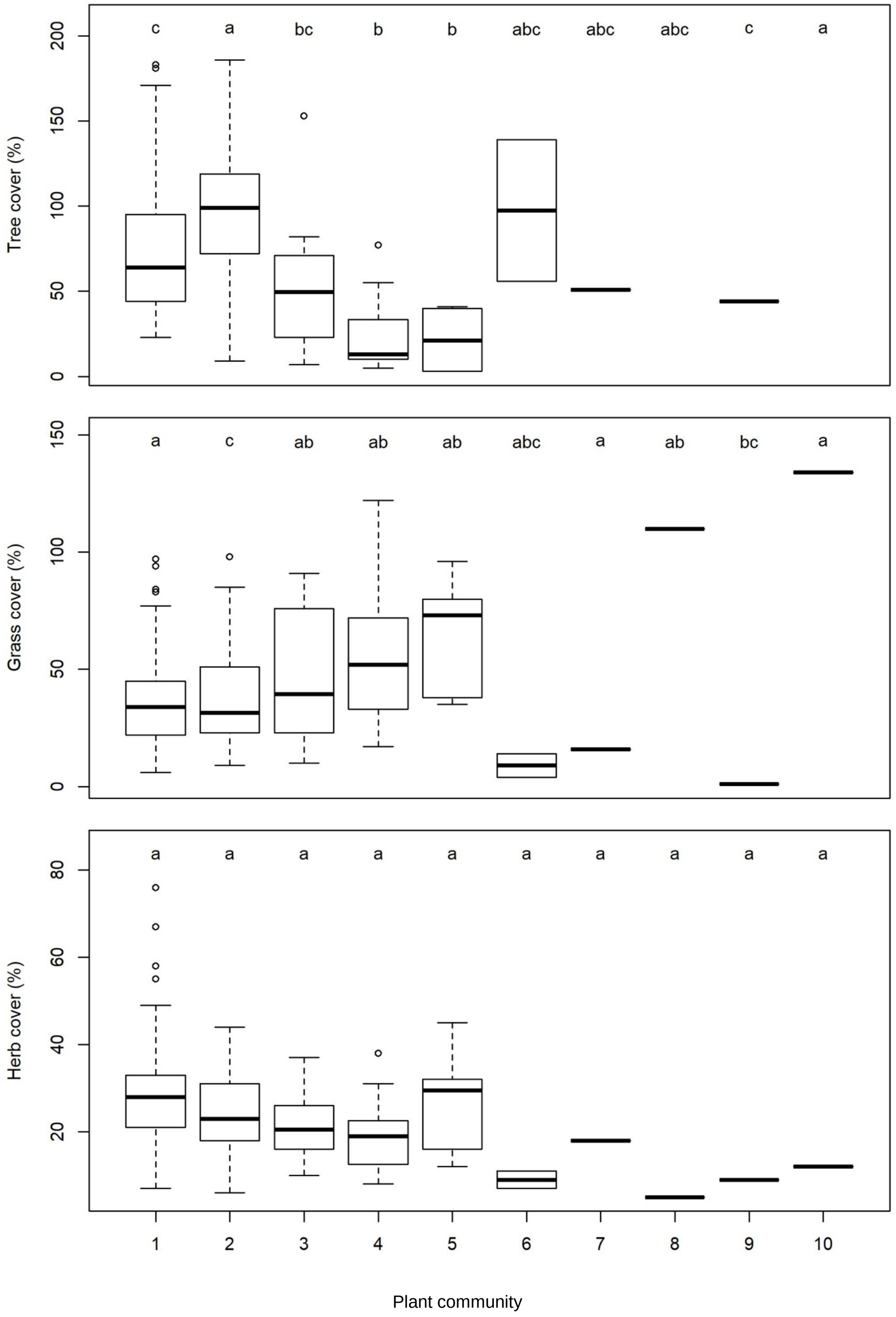


Figure 10. Average tree, grass and herb cover within the ten terrestrial communities in Lapalala Wilderness Nature Reserve. Thick lines indicate median values, boxes show interquartile ranges, whiskers are ranges, and empty symbols are outliers. Significant relationships are indicated by letters, with communities not sharing a common letter differing significantly at alpha = 0.05.

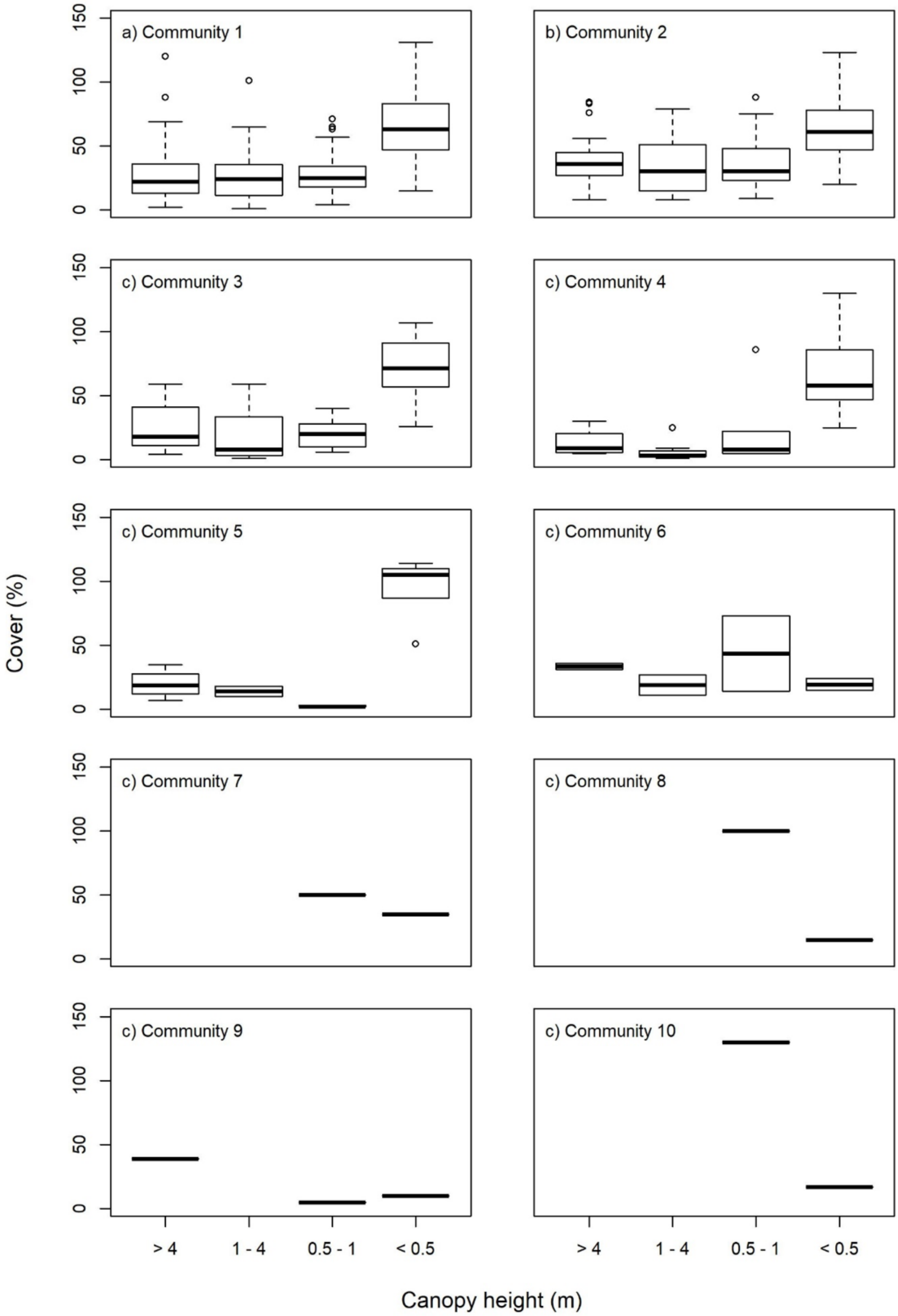


Figure 11. Average cover for each canopy level within each of the ten terrestrial vegetation units. Thick lines indicate median values, boxes show interquartile ranges, whiskers are ranges, and unfilled symbols are outliers.

Environmental drivers

Distance-based Redundancy Analyses (Figure 12) showed that species composition across LWNR was significantly related to 12 environmental variables: sand (particle size > 500 ɥm; p = 0.1), elevation (p = 0.01), sand (total before separating into fractions, p = 0.035), phosphorus (p = 0.015), stone cover (p = 0.005), carbon (p = 0.005), leaf litter (p = 0.005), calcium (p = 0.03), pH (p = 0.025), sand (particle size 53-100 ɥm; p = 0.065), potassium (p = 0.005) and bare ground (p = 0.005). However, the total proportion of variation in species composition explained by these variables was only 15%. The communities identified in the classification do not clearly separate in the NMDS ordination (Figure S4), with some communities showing greater distance between relevés within the community than the distance to relevés in other communities (see e.g. Community 4 in Figure 12).

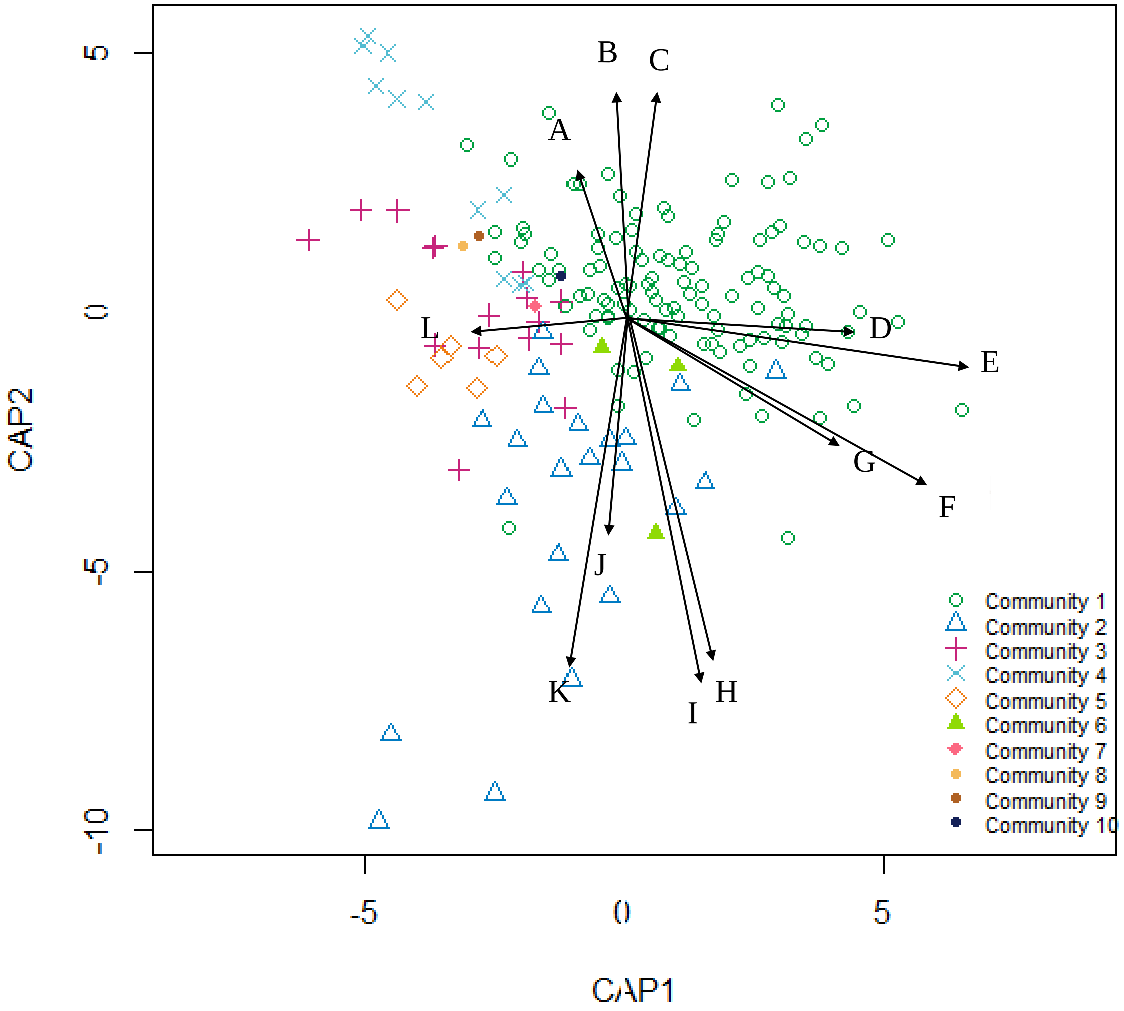


Figure 12. db-RDA ordination illustrating the relationship between species composition (with points representing each of the 180 relevés and colours illustrating the plant communities) and environmental variables (illustrated by arrows). Only significant environmental variables are shown. A = Sand (% particle size > 500 ɥm), B = Elevation (m), C = Sand (%), D = Phosphorus (%), E = Stone cover (%), F = Carbon (%), G = Leaf litter (%), H = Calcium (%), I = pH ($CaCl_2$), J = Sand (% particle size 53 – 100 ɥm), K = Potassium (%), L = Bare ground (%).

The relationship between each predictor and the occurrence of the five well-sampled communities was investigated and 21 variables were identified to have a significant effect on the occurrence of plant communities (Figure 13). Most of these variables were related to soil texture (n = 10) and soil nutrient content (n = 7). Loamy coarse sand (86 relevés) and coarse sandy loam (69 relevés) were the most common soil type in the reserve, found in almost all the communities (summarised in Table 2). However, Community 2 had soil properties most different to the rest of the communities (which were all roughly similar). Notably, the Community 2 had lower sand content (with the sand generally having smaller particle size) and higher loam content (Figure 13). The nutritional content of the soil in Community 2 was also generally greater than in the other communities, with higher levels of magnesium, potassium, sodium, calcium and carbon (Figure 13). Community 2, as well as Community 5, had a higher pH than the other communities. Lastly, elevation, stone cover, bare ground and distance from water also tended to differ between the plant communities, but none of these variables clearly distinguished any of the communities (Figure 13).

Table 2. Soil type distribution across the 10 plant communities in Lapalala Wilderness Nature Reserve. The numbers in the body of the table are number of relevés.

	Community										
Soil type	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Total**
Coarse Sand	6		4		2						12
Sandy Loam	8	12	1		1					1	23
Coarse Sandy Loam	32	4	1	4	1	1		1			44
Fine Sandy Loam		1									1
Sandy Clay Loam	2	2									4
Loamy Sand	8			1							9
Loamy Coarse Sand	61	3	10	6	2	2	1		1		86
Loam		1									1

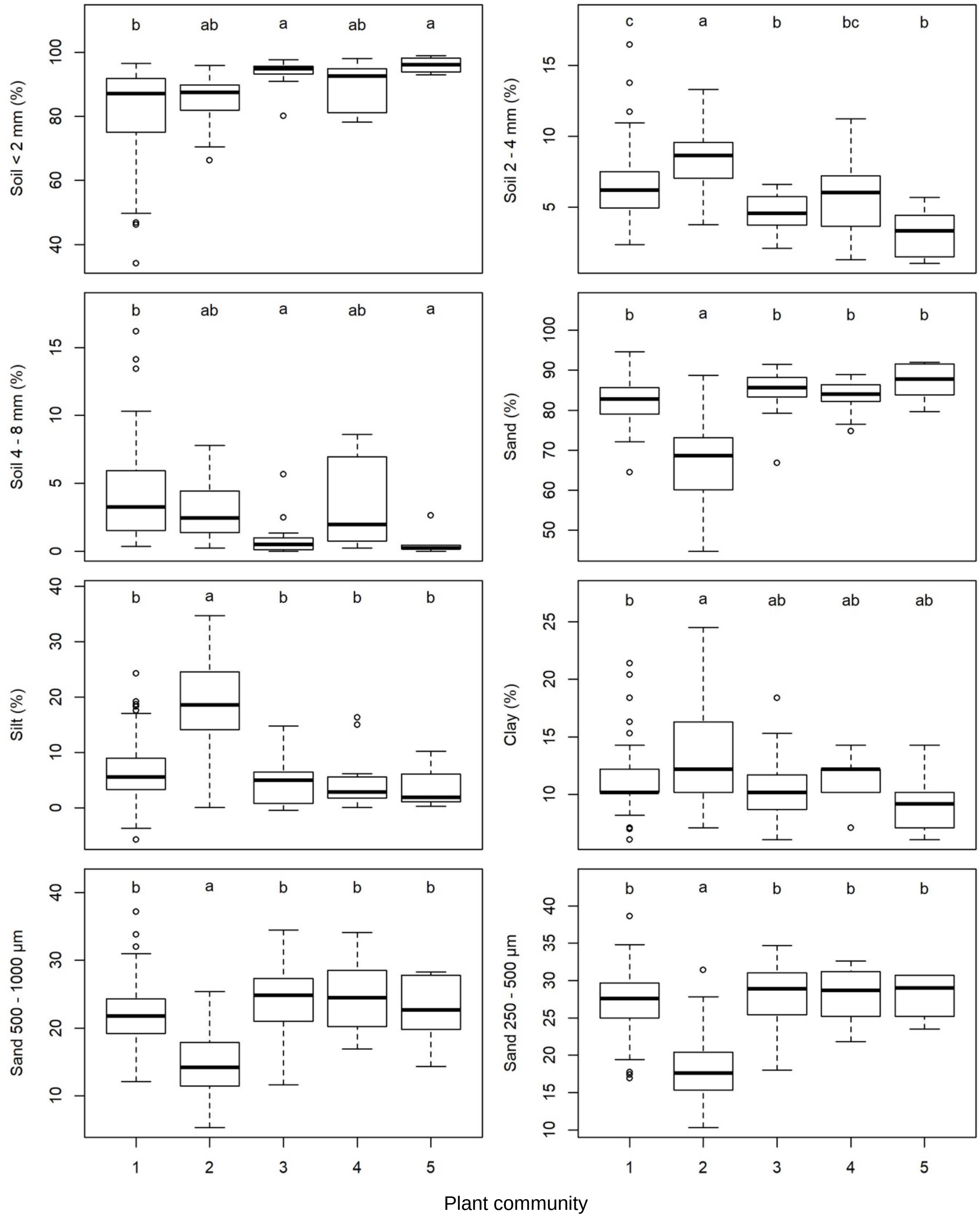


Figure 13. The relationship between environmental variables and the occurrence of the five well sampled plant communities. In the boxplots, the thick lines indicate median values, boxes show interquartile ranges, whiskers are ranges, and empty symbols are outliers. Only environmental variables that showed a significant relationship community occurrence are plotted here. The communities not sharing a common letter differ significantly at alpha = 0.05.

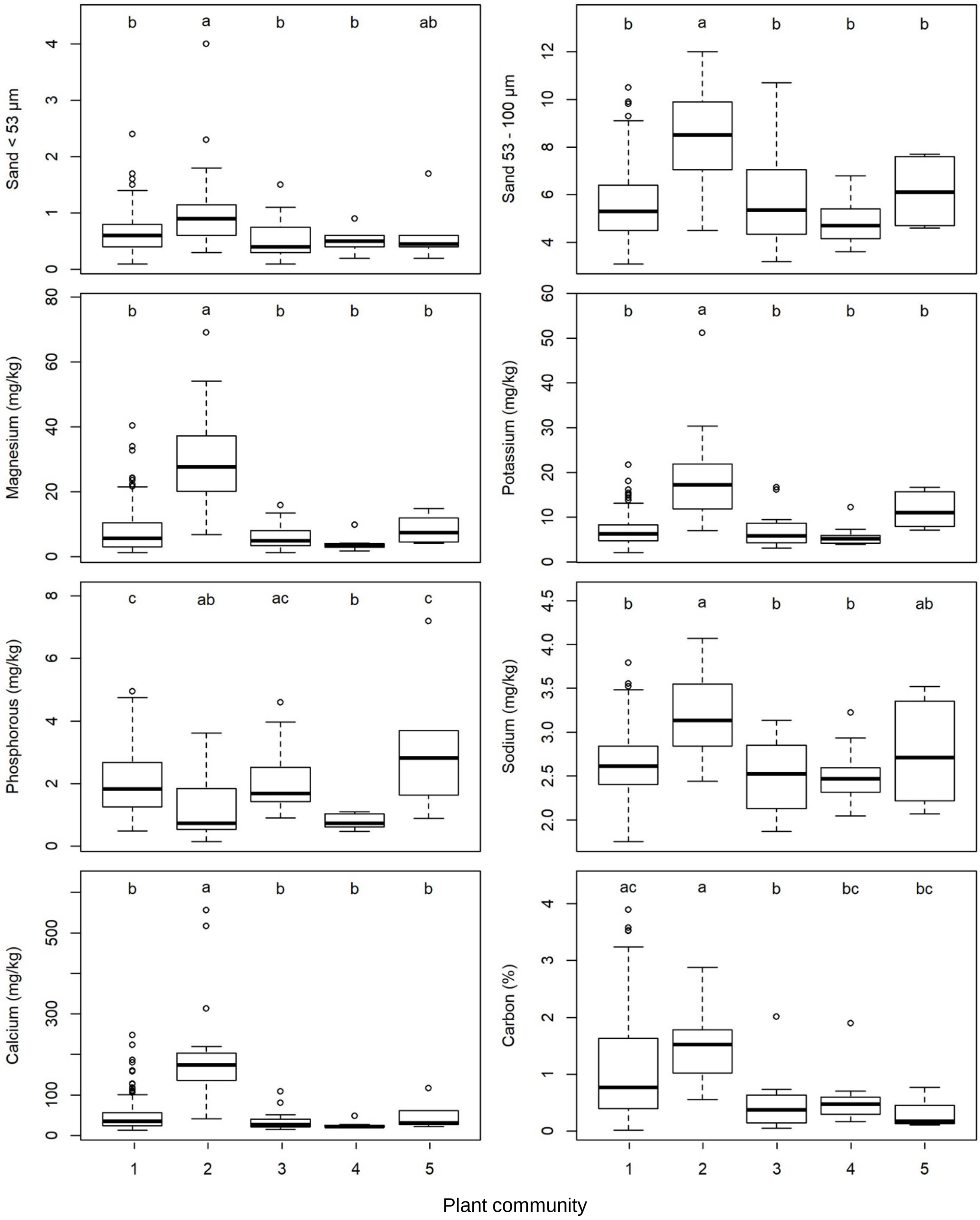


Figure 13. Continued

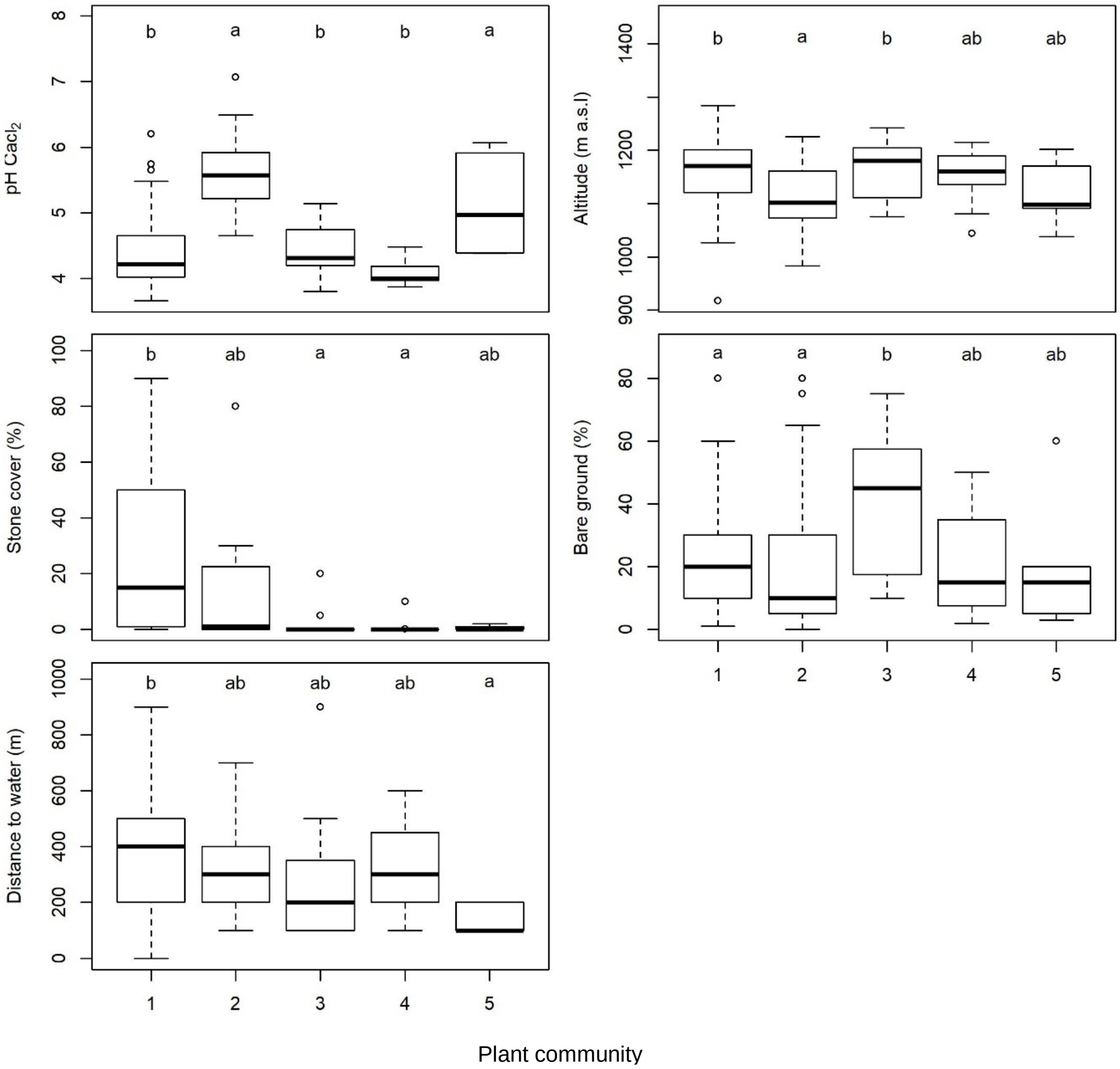


Figure 13. Continued

Community Descriptions

Community 1: *Combretum molle-Schmidtia pappophoroides* woodland

This woodland community (Figure 14) was the dominant vegetation type in LWNR, comprising 65% of the sampled relevés. It was found across the entire reserve and was not strongly associated with any particular environmental variable, although it tended to occur at higher elevations with loamy coarse sand or coarse sandy loam and high stone cover. There was a mean (± SD) of 50 (± 12) species per relevé in the community and 281 species were observed across all relevés (with an estimated total richness of 313 species). Diagnostic species are *Combretum molle, Diplorhynchus condylocarpon, Elephantorrhiza burkei, Lannea discolor, Pseudolachnostylis maprouneifolia, Pterocarpus rotundifolius* (tree), *Loudetia simplex, Schmidtia pappophoroides* (grass), *Harpagophytum procumbens,* and *Xerophyta retinervis* (herb). Prominent and dominant species are reported in full in Table S5.

Community 1 was subsequently subdivided into eight sub-communities. Diagnostic species were determined for the four sub-communities which comprised more than one relevé (Table S6). All sub-communities share the same diagnostic species as Community 1, and these are therefore not listed. The four well-sampled sub-communities are:

Sub-community 1: This sub-community was the largest, comprising 79% of Community 1, and was therefore the most abundant plant community within LWNR. Diagnostic species for this sub-community are *Grewia monticola* (tree), *Gisekia africana*, *Indigastrum costatum, Ipomoea magnusiana, Melhania prostrata, Tephrosia purpurea,* and *Xenostegia tridentata* (herb).

Sub-community 2: This sub-community comprised 13% of relevés within Community 1. Diagnostic species are *Brachiaria deflexa* (grass), *Asclepias burchellii, Asparagus* sp., *Chlorophytum recurvifolium, Cienfuegosia digitata,* and *Senecio barbertonicus* (herb).

Sub-community 3: This sub-community only comprised 5 % of the relevés within Community 1. Diagnostic species are *Lannea discolor, Euclea linearis* (tree), *Andropogon chinensis, Chrysopogon serrulatus, Eragrostis racemosa, Heteropogon contortus, Trichoneura grandiglumis, Themeda triandra* (grass), *Blepharis saxatilis,* and *Hemizygia canescens* (herb).

Sub-community 4: This sub-community was represented by only 3 relevés. Diagnostic species are *Grewia caffra*, *Senegalia burkei* (tree), *Aristida stipitata*, *Eragrostis rigidior*, *Sporobolus ioclados* (grass), *Indigofera ingrata*, *Limeum fenestratum*, *Nuxia oppositifolia*, and *Sida cordifolia* (herb).

Figure 14. Selected stands of the *Combretum molle*-*Schmidtia pappophoroides* woodland

Community 2: *Senegalia nigrescens-Heteropogon contortus* woodland

Twenty-three relevés were classified into this community and this woodland was, therefore, the second most common community in LWNR (Figure 15). This community was the most distinct in terms of environmental variables and tended to have a lower (and finer) sand content (although sandy loam was the most common soil type) and higher silt content. This community was more nutrient-rich than the other communities with higher levels of magnesium, potassium, calcium and carbon. There was a mean (± SD) of 50 (± 12) species per relevé, with 217 species observed across all relevés (and an estimated total richness of 312 species). Diagnostic species are *Ximenia americana*, *Berchemia discolor*, *Dombeya rotundifolia*, *Grewia flava*, *Heteropyxis natalensis*, *Senegalia nigrescens*, *Ziziphus mucronata, Dichrostachys cinerea, Grewia monticola, Grewia caffra, Gymnosporia buxifolia, Vachellia tortilis* (tree and shrub), *Enneapogon cenchroides, Enteropogon macrostachyus, Heteropogon contortus, Panicum deustum, Chrysopogon serrulatus, Cymbopogon pospischilii* (grass), *Chascanum hederaceum, Ruellia patula, Clerodendrum ternatum, Crabbea angustifolia, Lablab purpureus, Lantana rugosa,* and *Melhania prostrata* (herb).

Figure 15. Selected stands of the *Senegalia nigrescens-Heteropogon contortus* woodland.

Community 3: *Terminalia sericea-Aristida diffusa* woodland

Sixteen relevés were classified as *Terminalia sericea-Aristida diffusa* woodland (Figure 16). In general, this community had loamy coarse sand and a significantly higher cover of bare ground than the two most widespread communities. There was a mean (± SD) of 40 (± 10) species observed per relevé and a total of 168 species observed (and an estimated total richness of 221 species) across all relevés. Diagnostic species are *Euclea natalensis, Fadogia homblei, Terminalia sericea* (tree and shrub), *Aristida diffusa, Digitaria eriantha, Pogonarthria squarrosa, Eragrostis rigidior* (grass), and *Limeum fenestratum* (herb).

Figure 16. Selected stands of the *Terminalia sericea-Aristida diffusa* woodland.

Community *4: Burkea africana-Eragrostis gummiflua* woodland

Eleven relevés were classified into this woodland community (Figure 17). This community was generally found on loamy coarse sand and coarse sandy loam and had the lowest tree cover and the lowest mean soil pH (although not significantly lower than in Community 1). There was a mean (± SD) of 29 (± 8) species observed per relevé and a total of 116 species observed (and an estimated total richness of 169 species) across all relevés. Diagnostic species are *Faurea saligna* (tree), *Eragrostis gummiflua, Sporobolus stapfianus, Eragrostis racemosa* (grass), *Cyperus esculentus* (sedge), *Cordylostigma virgata, Chamaecrista mimosoides, Helichrysum cerastioides, Indigastrum costatum, Agathisanthemum bojeri, Eriospermum porphyrovalve,* and *Oxalis obliquifolia* (herb).

Figure 17. Selected stands of the *Burkea africana-Eragrostis gummiflua* woodland**.**

Community 5: *Cynodon dactylon-Eragrostis patentipilosa* grassland

Six relevés were classified into this grassland community (Figure 18), with these relevés all being consistently observed in flat and previously disturbed areas (i.e. likely abandoned agricultural fields that had been previously ploughed). This community was also generally found closer to water channels and had lower soil carbon and clay content and higher soil potassium content than other communities. Community 5 was dominated and characterised by low lying vegetation (i.e. short grasses and herbs) as well as high grass cover and low tree cover. There was a mean (± SD) of 28 (± 7) species observed per relevé and a total of 72 species observed (and an estimated total richness of 98 species) across all relevés. Diagnostic species are *Gardenia volkensii* (tree and shrub), *Cynodon dactylon, Eragrostis patentipilosa*, *Sporobolus festivus*, *Melinis nerviglumis*, *Tragus berteronianus, Urochloa panicoides* (grass), *Acanthospermum hispidum, Gomphrena celosioides*, Portulaca quadrifida, Schistostephium crataegifolium, Sida cordifolia, Solanum campylacanthum, Boerhavia repens, Cleome monophylla, Dicerocaryum eriocarpum, Tribulus terrestris, Alternanthera pungens*, Bulbostylis hispidula, Datura ferox*, Gisekia africana, Hirpicium bechuanense, Monsonia angustifolia, Oxygonum sinuatum, Satureja biflora, Seddera capensis,* and *Waltheria indica* (herb).

Figure 18. Selected stands of the *Cynodon dactylon-Eragrostis patentipilosa* grassland.

Communities 6 through 10 were all poorly sampled, with three or fewer relevés sampled per community (i.e. together comprising < 4% of samples). Some of these relevés were identified during the ad-hoc sampling and were noticeably different in the field from the surrounding vegetation. Due to the low number of relevés in these communities, diagnostic species were not determined, and prominent species are reported instead.

Community 6: *Grewia monticola-Vachellia nilotica* woodland

Three relevés were classified into this community (Figure 19). There was a mean (± SD) of 34 (± 10) species observed per relevé and a total of 74 species observed across all relevés. This community had the highest median tree cover and very low cover of grass and herbs. Prominent species were identified as *Grewia monticola, Grewia caffra, Bridelia mollis, Kirkia acuminata, Strychnos madagascariensis, Vachellia sieberiana, Senegalia burkei, Acacia fleckii, Vachellia nilotica* (tree and shrub), *Aristida stipitata, Helictotrichon turgidulum* (grass), *Pavonia transvaalensis, Euphorbia neopolycnemoides, Commelina erecta, Gloriosa rigidifolia, Thunbergia neglecta, Clerodendrum ternatum, Vitex rehmannii, Harpagophytum procumbens,* and *Coccinia sessilifolia,* (herb).

Figure 19. Selected stands of the *Grewia monticola*-*Vachellia nilotica* woodland.

Community 7: *Euclea linearis* shrubland

This shrubland community was represented by only one relevé, containing 27 species (Figure 20). Prominent species are *Euclea linearis* (which was also dominant), *Ochna serrulata* (tree and shrub), *Brachiaria serrata*, *Microchloa caffra* (grass), *Cordylostigma virgata, Hermannia quartiniana, Limeum viscosum, Xenostegia tridentata, Dipcadi marlothii,* and *Polygala amatymbica* (herb).

Figure 20. The stand of the *Euclea linearis* shrubland.

Community 8: *Cymbopogon pospischilii* grassland

This grassland community was represented by only one relevé, comprising 11 species (Figure 21). Prominent species are *Cymbopogon pospischilii* (which also dominates this community with 100% cover; grass)*, Dicerocaryum eriocarpum,* and *Senecio barbertonicus* (herb).

Figure 21. The stand of the *Cymbopogon pospischilii* grassland.

Community 9: *Vitex obovata-Phyllanthus parvulus shrubland*

This shrubland community was represented by only one relevé (Figure 22), containing 14 species. Prominent species are *Euclea natalensis, Vitex obovata, Ochna pulchra* (tree), *Zornia milneana, Indigofera daleoides,* and *Felicia mossamedensis* (herb).

Figure 22. The stand of the *Vitex obovata-Phyllanthus parvulus* shrubland.

Community 10: *Andropogon eucomus-Eragrostis heteromera* grassland

This grassland community was represented by only one relevé (Figure 23), containing 18 species. Prominent species are *Arundinella nepalensis, Andropogon huillensis, Eragrostis heteromera, Andropogon eucomus, Setaria sphacelata, Urochloa panicoides* (grass), *Gladiolus dalenii, Hypericum lalandii, Monopsis decipiens, Oxalis corniculate**, Senecio erubescens, Hilliardiella elaeagnoides* (herb), *Fuirena pubescens,* and *Cyperus esculentus* (sedge).

Figure 23. The stand of the *Andropogon eucomus-Eragrostis heteromera* grassland.

Community 11: *Phragmites mauritanus-Miscanthus junceus* reedbed

This vegetation type was not formally sampled due to a high risk of encountering Cape Buffalo in the reedbeds (Figure 24). It was, however, widely observed that the areas along the perennial rivers were characterised, and dominated, by the reeds *Phragmites mauritanicus* and *Miscanthus junceus.*

Figure 24. Selected stands of the *Phragmites mauritanus-Miscanthus junceus* reedbed.

Vegetation Mapping

Four plant communities were successfully mapped using satellite imagery and environmental data (Figure 25). These were Community 1: *Combretum molle-Schmidtia pappophoroides* woodland (comprising 66% of the mapped area), Community 2: *Senegalia nigrescens-Heteropogon contortus* woodland (26%), Community 3: *Terminalia sericea-Aristida diffusa* woodland (3 %) and Community 5: *Cynodon dactylon-Eragrostis patentipilosa* grassland (5 %). These four units made up a substantial proportion of the sampled relevés (162 of 180 relevés), with the other six units consisting of only 18 relevés collectively. The overall accuracy of the map was high at 70 %. Community 1 had a higher accuracy with very few user and producer errors (Table 3). However, the accuracy for the other communities (represented by fewer relevés; Communities 2, 3, and 5) was low. As a result, the Kappa index accuracy was only 40%.

Table 3. Kappa matrix for the accuracy assessment of the map of the vegetation of Lapalala Wilderness Nature Reserve. Predicted data is the community assigned on the vegegtation map and actual data is the community assignment at the same location in the field.

		Actual data					
		Commmunity 1	Commmunity 2	Commmunity 3	Commmunity 5	Total	User's accuracy
Predicted data	Commmunity 1	103	18	13	9	143	0.72
	Commmunity 2	5	16	2	1	24	0.67
	Commmunity 3	2	1	4	0	7	0.57
	Commmunity 5	0	1	1	5	7	0.71
	Total	110	36	20	15	181	
	Producer's accuracy	0.94	0.44	0.20	0.33		0.71
	Agreement	103.00	16.00	4.00	5.00	128.00	
	By chance	86.91	4.77	0.77	0.58	93.03	

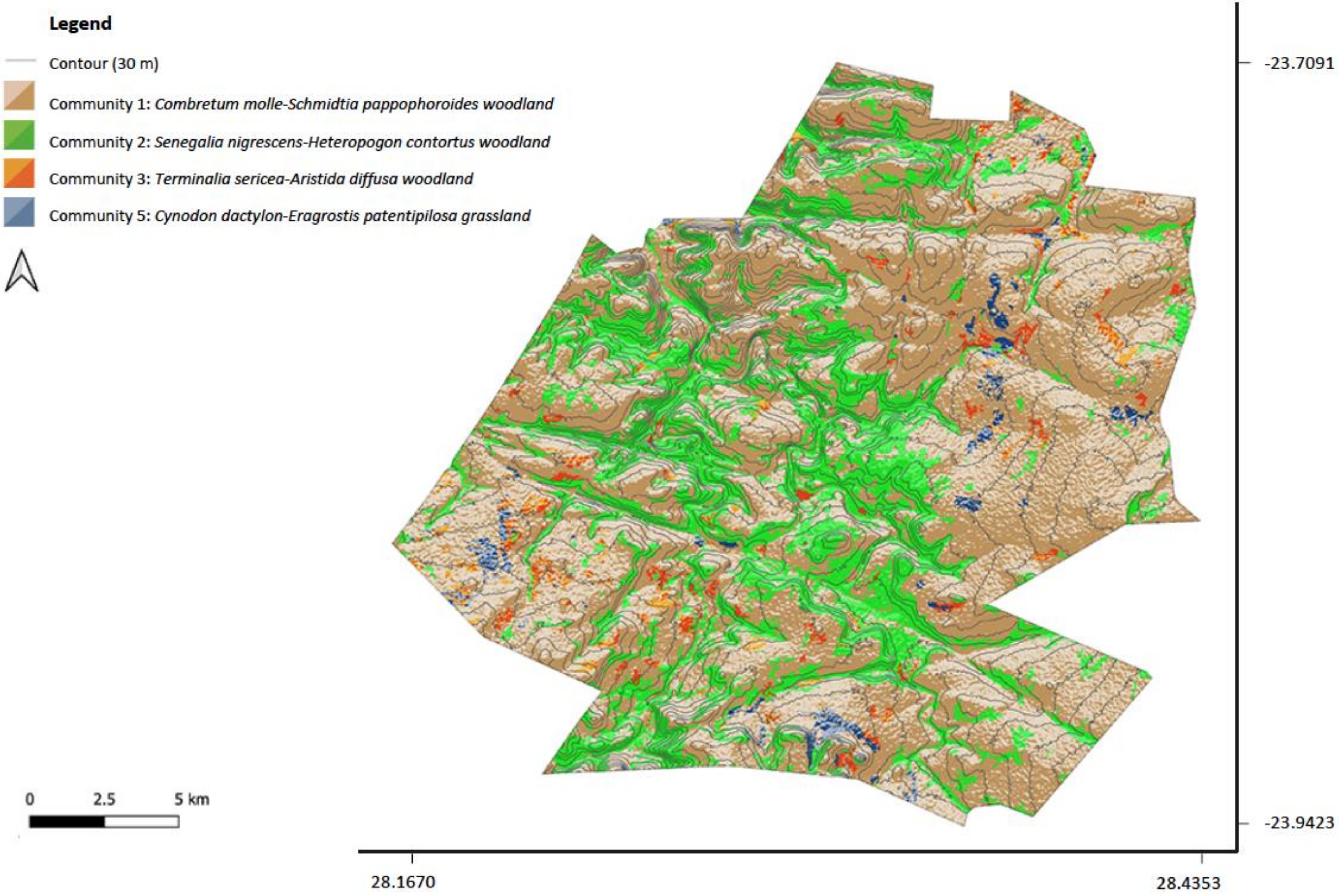


Figure 25. Vegetation map of Lapalala Wilderness Nature Reserve. Colour variation indicates hill-shading. Contours are at 30 m intervals. There are 6 plant communities that could not be mapped using the model.

Discussion

The vascular plant species richness of LWNR was high with 355 species recorded and a total estimated richness exceeding 500 species. This is on par with surrounding areas, with, for example, 445 species recorded at Welgevonden Game Reserve, a similar sized conservation area also located in the Waterberg, c. 60 km from LWNR (Tamryn Venter, pers. comm. August 2021). However, vascular plant species richness is heterogeneously distributed across LWNR, with richness within relevés ranging from 11 to 86 species.

The vegetation of LWNR was classified into eleven communities of which just two are estimated to cover c. 92 % of LWNR. Only the ten terrestrial communities were considered in analyses and are discussed further. The species richness of the five most sampled plant communities ranges from 281 and 217 (in the two dominant communities) to 72. The ten terrestrial communities did not separate out clearly in terms of species composition, with there being a low number of species unique to individual communities and 42 species common to all five of the most sampled communities. Additionally, environmental variables did not differ significantly between most plant communities and could not accurately predict the occurrence of some plant communities across the extent of LWNR.

Few truly diagnostic species could be identified for the majority of the plant communities in LWNR. By definition, diagnostic species should be associated with only one community and found rarely, or not at all, in other communities (De Cáceres and Wiser, 2012; Peinado et al., 2013). In this study, only seven of the 82 diagnostic species were limited to only one community. Indeed, 10 of the diagnostic species occurred in more than 50 % of relevés outside of its diagnostic community, with *Digitaria eriantha* being found in 71 % of relevés outside of its association (Community 3). This makes using the diagnostic species alone to identify community types in the field difficult and potentially inaccurate. Therefore, here prominent and dominant species are included with the diagnostic species to account for the large degree of overlap in species composition between plant communities. Prominent species take into account that there is an overlap of species between communities but the total cover of the prominent species is much greater in its assigned community than the other communities. For example, *Heteropogon contortus* is a prominent species in community 2 where it occurs in the majority of relevés (19 out of 26 relevés) with a mean cover of 10 %

per relevé. This grass is present in another 60 relevés outside of Community 2, but rarely occurs with a cover > 2 % in any other relevé. Dominant species enhance community identification when used with the diagnostic and prominent species. Dominant species do not specifically serve to distinguish communities, but help to describe the main vegetative components of communities. Calculations of dominance are based within a community and not between them and so species can be dominant in more than one community. For example, *Phyllanthus parvulus* is dominant in Communities 1, 2, 3, 4, and 9. Problematically, some species are found in different categories in different communities, e.g. *Grewia caffra* is diagnostic for Community 2, prominent in Community 6 and dominant in Communities 1, 2, 3 and 6. Due to the lack of distinction in species composition between the communities, using the diagnostic, prominent and dominant species together is the best way to differentiate the communities of LWNR, especially when in the field.

Plant communities

The LWNR landscape is dominated by Community 1 (*Combretum molle-Schmidtia pappophoroides* woodland), which was recorded in c. 65 % of relevés and is estimated to cover c. 66 % of the reserve. This community, which includes *Diplorhynchus condylocarpon* as a dominant species, appears to be equivalent to typical Waterberg vegetation (see Mucina and Rutherford, 2006) and similar vegetation is frequently found in other nearby reserves (e.g. Marakele National Park; Van Staden et al., 2005). No environmental variables clearly distinguished plant Community 1 from the other less common plant communities. Indeed, as this community covers the majority of LWNR, it tends to be found in most of the differing environmental combinations in the reserve and occurs across a broad range of each of the environmental variables. For example, Community 1 occurs across the entire range of soil carbon (0-4 %) observed in LWNR, while other communities' ranges are much smaller for this variable.

Plant Community 2 (*Senegalia nigrescens-Heteropogon contortus* woodland) is widespread in LWNR and is found mostly (but not exclusively) in close proximity to valleys and was seldom recorded on plateaus. While this relationship with topography was not clear from the data, this community did tend to occur at lower elevation than the other widespread communities (Communities 1 and 3). This community is the only community that differed in terms of soil texture (with a higher proportion of finer sand particles and much more silt) and soil nutrients (with higher levels of carbon, calcium, sodium, potassium and magnesium) from the other plant communities. Indeed, even visually, soils in this community tended to be redder in colour than in the other communities. The higher nutrient levels in this community potentially account for the unique species found only in this community, as nutrient-rich savannas tend to have fine-leaved woody species (Scholes, 1990) and more palatable vegetation. This was seen with species such as *Vachellia tortilis, Senegalia nigrescens* and *Dichrostachys cinerea* being diagnostic or dominant in this area as well as being fine-leaved and good for browsing (Cooper and Owen-Smith, 1985; Hassen et al., 2009; Mandinyenya et al., 2019)**.** This community appeared heavily grazed, and potentially even overgrazed, in some areas. Certainly, it was in this community that most large herbivores were observed (pers. obs.).

Stands of Communities 1 and 2 have quite different vegetation structure, with Community 1 comprising shorter "bushier" trees with taller and denser grass patches between the trees. In contrast, Community 2 typically had a taller and more complete canopy cover with shorter and much sparser grass cover under the trees. However, the data collected does not reflect these differences, and show the two communities to be similar in structure (see Figures 10 and 11). This disparity between observations and recorded data may be due to the coarse plant height classes used. Fine-scaled data, with more canopy layer categories (or more exact records of canopy heights) may be necessary to more accurately document the patterns observed in the field. Alternatively, using new remote sensing approaches such as Lidar to quantify vegetation structure may offer an efficient and accurate test of differences in vegetation structure between the plant communities of LWNR (Nagendra et al., 2013; Guo et al., 2017; Zimbres et al., 2020).

Community 3 (*Terminalia sericea-Aristida diffusa* woodland) and Community 4 (*Burkea africana-Eragrostis gummiflua* woodland) were scarcer in the surveyed area, with Community 3 mapped across c. < 10 % of LWNR. *Terminalia sericea-Burkea africana* is one of the plant communities identified by Mucina and Rutherford (2006) for the Waterberg region, and these two tree species are diagnostic and prominent species in Community 3 and 4, respectively, but are also found in many of the other communities in LWNR. In Marakele National Park, the *Faurea saligna-Setaria sphacelata* community (Van Staden, 2002) has *Terminalia sericea* as a diagnostic species, and is dominated by *Burkea africana*, *Dichrostachys cinerea* and *Faurea saligna*. These species are important species in Community 3 (*Terminalia sericea; Dichrostachys cinerea*) and Community 4 (*Burkea* *africana; Faurea saligna*). *Terminalia sericea* and *Burkea africana* are also associated with each other in Welgevonden Game Reserve, another nearby reserve in the Waterberg. This difference can potentially be explained by competition, which has been previously shown to influence the spacing of these tree species (see Smith and Grant, 1986). Previous studies into *Terminalia sericea* distribution suggests soil moisture plays a key part in determining the presence and distribution of the species (Katjiua and Ward, 2006). With this species being an important important species for browsers (Katjiua and Ward, 2006) and widely spread in LWNR (average cover of 25 % within Community 3, maximum cover = 100 %), investigations into this species and its associated community may be beneficial for managing browsers (especially for game farming purposes).

Community 5 (*Cynodon dactylon-Eragrostis patentipilosa* grassland) was most common in areas that appeared to have previously been ploughed (i.e. used for agriculture), explaining the frequent occurrence of species that are typical of disturbed or heavily grazed areas, e.g. *Cynodon dactylon* (Amundson et al., 1995), *Tragus berteronianus* (Backéus et al., 1994; Kassahun et al., 2009) and *Gomphrena celosioides** (Chen and Li, 2012). Due to ploughing (and possibly fertilization), the soils of these areas were expected to differ from areas that had not been used for cultivation (Scholes, 1990; Compton et al., 1998; Smet and Ward, 2006). However, this community did not significantly differ from other communities in any of the soil variables. Additionally, while Community 5 looked very different in vegetation structure from the other well-sampled communities, with low growing vegetation and few trees, and had many diagnostic species, this plant community still shared many species with the surrounding vegetation. Indeed, based on species composition this community did not separate out as clearly from the rest of the plant communities as would be expected from its vegetation structure. It appears, therefore, that ecological succession is causing the vegetation in these areas to gradually shift back to the natural species composition of the surrounding areas. Indeed, a previous study has shown some areas (especially under trees and shrubs) within previously disturbed lands are beginning to closely resemble surrounding vegetation in LWNR (Ruwanza, 2018). As eco-tourism is a key use of this landscape (and a major source of income), these open areas are beneficial for game sightings. As such, there is an obvious pragmatic reason to keep these areas in an open state, but care should be taken to ensure that invasive species are not present or benefitting by management actions in this community.

All of the rarer communities, which were only sampled by one or two relevés, appear to represent true plant communities (i.e. they are not ecotonal or of anthropogenic origin). Although infrequently sampled (and chiefly sampled as a result of the ad-hoc relevés), these rare communities were observed at other sites in LWNR during the initial vegetation survey (pers. obs.) and during the mapping validation surveys (pers. comm., Peter le Roux February 2021). Community 6 (*Grewia monticola-Vachellia nilotica* woodland) is characterised by dense clumps of trees, mainly *Grewia* species, with sparse undergrowth cover. These thick clumps were seen in many places in LWNR, but were very spatially localized, and could easily be missed when sampling randomly. These clumps always appeared to be centred around a large tree, in otherwise open areas, and it is possible that these trees are demonstrating nurse effects (Manning et al., 2006; Ruwanza, 2018) and potentially initiating the formation of a bush clump (Jamison-Daniels et al., 2021). Termite mounds have also been shown to play an important role in establishing bush clumps in savanna ecosystems (Joseph et al., 2012). Despite only being sampled in a single relevé, Community 7 (*Euclea linearis* shrubland) was observed in three other very distinct locations in LWNR. This community was dominated by *Euclea linearis* shrubs, with few other species which tended to be small in size.

Another of the poorly sampled plant communities was the *Cymbopogon pospischilii* grassland (Community 8), which occured in small areas with dense growth of *Cymbopogon pospischilii*. It was observed in at least three areas across the reserve, although only recorded once. Studies have suggested that fire (Barko and Smart, 1979, Snyman, 2015) and increased herbivory (Radloff et al., 2014; Pellegrini, 2016) can result in an increase in *Cymbopogon pospischilii* grass cover, however, no evidence suggests that this is the case in LWNR. *Vitex obovata-Phyllanthus parvulus* shrubland (Community 9) was also poorly sampled and appears to be a response to overgrazing or to occur chiefly along the borders of old fields. This community was not seen elsewhere in the reserve during sampling, but due to the similarity it has with other communities (e.g. it is dominated by *Terminalia sericea* and all other species recorded in this community are common in other communities, including *Combretum apiculatum* and *Phyllanthus parvulus*), it could have been easily overlooked. Lastly, the relevé representing the *Andropogon eucomus-Eragrostis heteromera* grassland appeared to have been sampled in a wetland (or, at least, some form of a seep), as the soil was quite damp even when sampling late in the summer season. Additionally, the species recorded here are typically associated with wet areas, such as *Andropogon eucomus*

(Anderson, 1966) and *Cyperus esculentus* (Barko and Smart, 1979). It is likely that this plant community occurs in vleis (or marshy depressions) in LWNR, which remained undetected in this sampling season due to very late and low rainfall in the sampling period. These small and unique communities add variation and heterogeneity to the landscape of LWNR and potentially provide unique habitats for wildlife and should be considered during management protocols.

Environmental variables

In total, environmental variables only explained 15% of the variation observed in plant composition, with soil properties being the strongest drivers of species composition within LWNR. Other studies also show that environmental variables can have a low explanatory power for vegetation variation, with soil tending to have the strongest effect (e.g. Mostert et al., 2008; Baldeck et al., 2014). Soil texture, pH, and soil nutrients had a significant (albeit relatively weak) impact on the vegetation composition in this study. In general, it appears that Community 2 had soil properties most different from the rest of the communities, which were otherwise all roughly similar. Also, during field work, it was observed that in some areas of the reserve many small conglomerates (soil particle size > 8 mm) covered the soil surface. This may be a driver of vegetation structure, as the conglomerates could be acting as a potential “rock mulch”, reducing herb growth as well as decreasing water loss and run-off (important for such a dry and sandy environment; Poesen et al., 1990). However, the cover of substrate larger than 8 mm had no significant influence on the vegetation. Therefore, while soil properties appear to contribute to determining the location of Community 2, what environmental conditions are driving the variation seen in the other communities is still largely unclear. Topography can strongly affect soil structure and quality (Kokulan et al., 2018; Li et al., 2020), but in this study, the topographical variables measured had little effect on the vegetation. Other soil-related variables, such as soil depth (and rooting depth), soil moisture, evapotranspiration etc., and other geological variables (including land-forms and rock-type) might be playing a part in the variation seen in LWNR (Kambatuku et al., 2013; Ward et al., 2013; Holdo and Brocato, 2015).

Many variables that are known to be related to variation in vegetation structure and composition showed no effect on the vegetation of LWNR. For example, aspect (Holland and Steyn, 1975; Baldeck et al., 2014), slope (Lawson et al., 1968; Holland and Steyn, 1975), topographical wetness index (Holland and Steyn, 1975; Wu and Archer, 2005; Baldeck et al., 2014), topographical position index (Holland and Steyn, 1975; Hejcmanovā-Nežerková and Hejcman, 2006), fire (Govender et al., 2006; Staver et al., 2017) and potential solar radiation (Holland and Steyn, 1975; Kanniah et al., 2013) all had no effect on the vegetation of LWNR, despite being highlighted in other studies as affecting the distribution of vegetation types. These variables may have an effect on individual species distribution (Witkowski and O'Connor, 1996) within the reserve and it may be worth re-running analyses for important species (i.e. using a species response curves). Alternatively, more variables can also be included in future studies (e.g. soil depth and soil moisture, following Walker and Langridge, 1997; Mostert et al., 2008).

Application

The overall accuracy of the vegetation map for LWNR was 70 %, with Kappa index value which is well below the accepted threshold for mapping (Fleiss, 1971). The mapping accuracy was proportional to the size of the mapped community (and sample size in terms of number of relevés), with Community 1 having high accuracy and Community 2,3 and 5 having a much lower accuracy (Table 3). There are a few reasons why the mapping of these vegetation units displayed low accuracy. First, the plant communities in LWNR appear to be a mosaic, with a matrix of Community 1 and 2 containing smaller patches of vegetation from the other communities, resulting in many ecotones between communities. As a result, many species, including diagnostic and prominent species, are potentially found in multiple plant communities due to the interdigitation of communities. This means that the presence of these species alone cannot accurately determine the vegetation type. Secondly using vegetation indices (i.e., NDVI, SAVI) could potentially improve the mapping (ref). Experimenting with other methods of mapping plant communities that consider multiple variables (e.g. random forest, Support Vector Machine, maximum likelihood) may also improve the results (ref). Lastly, the resolution of the satellite imagery used was possibly relatively low resolution for such a diverse and varied landscape, especially as many patches of vegetation less than 20 x 20 m were observed in the field. This potentially means that, for example, small wetland areas or rocky outcrops (both which could represent unique vegetation types) may not be detectable from satellite imagery. Additionally, pixels of ecotones, which are likely fairly common within the mapped area given the mosaic nature of the vegetation in LWNR, have a high chance of being classified incorrectly at the low-resolution imagery used in this study (De Klerk et al., 2018).

Another limitation of the vegetation map was that six plant communities (Communities 4, 7, 8, 9, and 10) could not be mapped using the available data. This likely reflects that their distribution was so limited in LWNR that an inadequate number of relevés was sampled to provide calibration data for mapping. Finer resolution remotely sensed environmental data (e.g. potentially from a UAV instead of satellite data) would provide better resolution data and could, thereby, potentially increase the overall map accuracy (Zongjian, 2008; Crommelinck et al., 2017). Moreover, addressing the lack of data for several ecologically relevant field-quantified environmental variables (including soil nutrient and soil moisture data) across the extent of the reserve could also result in a more accurate vegetation map. For example, as soil characteristics appear to influence the distribution of plant communities, and, therefore, using an accurate high resolution soil type map (or soil nutrient map) could potentially produce a more accurate vegetation map of LWNR.

Overall, the understanding and description of the plant communities and vegetation map could be of considerable value for management and conservation within LWNR, allowing management programmes and conservation strategies to be refined and made more spatially explicit (Bezuidenhout, 2009). The plant communities in LWNR form a mosaic, with all mapped communities found throughout the reserve. In other words, there are no communities limited to any one specific area in LWNR. This, along with the low accuracy of the map, makes managing the communities as separate units challenging. However, as the plant communities do not represent clear management units - with species rarely found in only one community and communities are not confined to specific landforms or environmental variables, managing the communities as separate units is likely unnecessary (Bezuidenhout, 2009). Moreover, as none of the communities contained rare or endangered species, there is also little need to manage the communities differently for conservation purposes. However, consideration should be given to smaller communities when, for example, building new infrastructure to avoid losing large proportions of the rarer communities.

There are very few vegetation studies done in the Waterberg, with a vegetation classifcation of Marakele National Park being the only published study (Van Staden et al., 2005). The vegetation grouping seen in LWNR differs from Marakele in both vegetation structure and species composition. For example, Marakele contains forest communities with species such as *Podocarpus latifolius* and *Olea capensis*, which are absent from LWNR, and has common tree species such as *Englerophytum magalismontanum, Mimusops zeyheri, Diospyros* *whyteana* and *Canthium gilfillanii* which do not frequently occur, if at all, in LWNR. Moreover, species associated with each other in LWNR are commonly seen in different associations in Marakele (for example *Combretum molle* and *Diplorhynchus condylocarpon* occur in the same community in LWNR but occur in separate communities in Marakele). Understanding what drives the variation in vegetation across the Waterberg area can steer management protocols and conservation and can potentially facilitate broader scale vegetation mapping via remotely sensed data. Therefore, more studies of the plant assemblages of this region can improve vegetation management and conservation efforts for both the government and private landowners.

In conclusion, LWNR had 11 communities in total, one riparian and ten terrestrial communities. The terrestrial communities consisted of two main plant communities (*Combretum molle-Schmidtia pappophoroides* woodland and *Senegalia nigrescens-Heteropogon contortus* woodland), with eight rarer communities interspersed between them. There is no strong differentiation between the communities in terms of species composition and environmental variables. Mapping the area using satellite-derived variables was not very accurate due to weak relationships with satellite-derived variables but predicts a very heterogeneous mosaic of plant communities. Due to the paucity of vegetation studies and landscape-scale vegetation maps in the Waterberg, this study can form a stepping-stone to understanding vegetation patterns in this ecologically-important region.

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Appendix A: Spatial field design of vegetation sampling

To layout the relevé, the SE corner of the quadrat was located at pre-determined GPS coordinates. During the data collection process, the location of the relevé was moved to a new spot if one or more of the following occurs:

a. If the relevé shows signs of human disturbance or activities (e.g. it falls near an old homestead that was not marked on the map);
b. If the relevé falls within an area that has recently been, or shows sign of, bush-clearing activities;
c. If the relevé shows signs of any other major disturbance (e.g. a recent fire);
d. If the relevé is inaccessible by car or foot;
e. If the relevé is not homogenous (i.e. containing no change in physiognomy), with the most dominant plant taxa being approximately equally distributed across the relevé and no drastic changes in slope and aspect;
f. The relevé is not representative of surrounding vegetation (i.e. a small patch of vegetation that is different from all the surrounding vegetation within 10m);
g. If the relevé has more than 60% rock or bare soil cover (i.e. very little vegetation);
h. If the relevé contains a stream or river (running or dried-up).

If a relevé needed to be moved, the first corner was moved 50 m eastwards (unless that is in the direction of the disturbance, in which case the relevé was moved 50 m in the opposite direction of the disturbance).

Appendix B: Classification

Table S1. Ranking of the data analytical combinations examined in OptimClass. The Data analytical combinations are recorded in the order of: transformation, distance metric and clustering algorithm. The coefficient for Flexible beta clustering was -0.25. The rank was determined as an average of the methods performance across five Fisher's fidelity values ($p < 10^{-8}$, $p < 10^{-12}$, $p < 10^{-16}$, and $p < 10^{-20}$).

Rank	Data Analytical Combinations
1	No transformation; Bray-Curtis; Group average linkage
2	Logarithmic; Bray-Curtis; Group average linkage
3	No transformation; Relative Manhattan; Group average linkage
4	Square root; Bray-Curtis; Group average linkage
5	Presence absence; Relative Manhattan; Group average linkage
6	Square root; Relative Manhattan; Group average linkage
7	Logarithmic; Bray-Curtis; Flexible Beta
8	Logarithmic; Relative Manhattan; Flexible Beta
9	Presence absence; Bray-Curtis; Group average linkage
10	Square root; Euclidean; Ward
11	Presence absence; Bray-Curtis; Flexible Beta
12	Square root; Bray-Curtis; Flexible Beta
13	Logarithmic; Relative Euclidean; Ward
14	Floating cut level; Relative Euclidean; Ward
15	Presence absence; Relative Euclidean; Ward
16	Square root; Relative Manhattan; Flexible Beta
17	No transformation; Relative Euclidean; Group average linkage
18	Presence absence; Bray-Curtis; Complete linkage
19	No transformation; Bray-Curtis; Flexible Beta
20	Presence absence; Relative Manhattan; Flexible Beta
21	Logarithmic; Bray-Curtis; Complete linkage
22	Pseudo-species abundance; Jaccard; Flexible Beta
23	Pseudo-species abundance; Pearson's correlation; Ward
24	Pseudo-species abundance; Euclidean; Ward
25	No transformation; Relative Manhattan; Flexible Beta
26	Floating cut level; Euclidean; Ward
27	Presence absence; Euclidean; Ward
28	Logarithmic; Bray-Curtis; Single linkage
29	No transformation; Euclidean; Ward
30	Presence absence; Bray-Curtis; Single linkage

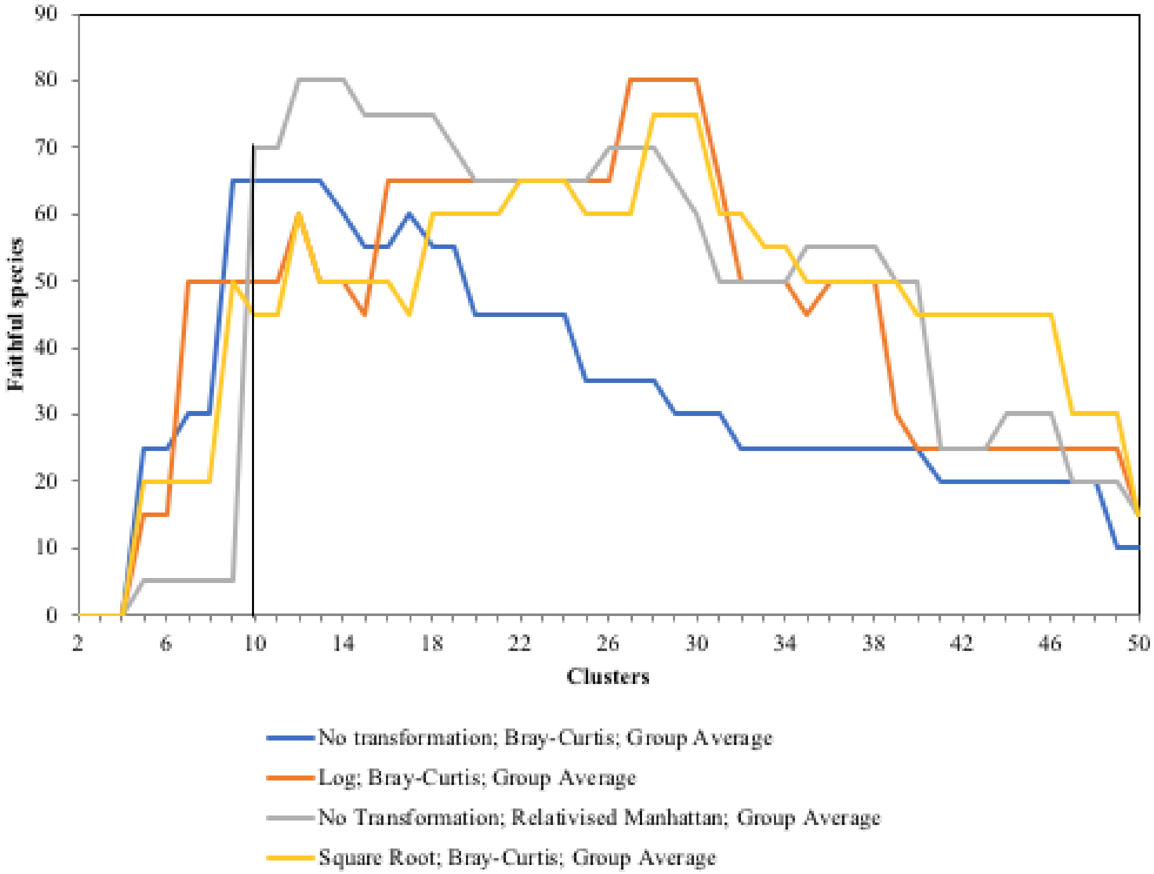

Figure S1. The number of faithful species presented for different numbers of clusters ranging from 2 - 50, as determined in JUICE. Ten clusters were determined to be the optimal number of clusters (illustrated by the vertical line) for this data set when using no transformation, Relative Manhattan Distance and UPGMA (Group average) clustering.

Table S2. List of all environmental variables initially considered as potential predictors in this study.

Heading	Description	Units
Altitude	Meters above sea-level.	m
Year_last_fire	The most recent fire detected by MODIS.	yyyy
Number_of_fires	The total number of fires detected by MODIS since 2002.	
Time_since_last_fire	The number of years since the last fire was detected by MODIS.	
Distance_from_water	Distance to the nearest water channel.	
Bare_ground	Represents % of releve covered by bare ground (i.e. not covered by leaf litter, woody debris, basal cover of live vegetation, etc.).	%
Leaf_litter	Represents % of releve covered by leaf litter (fallen and dying leaf matter on the floor of the releve).	%
Curvature	Positive values indicate convex, negative values are concave and 0 is flat (values rescaled by dividing by 10^7).	
Stone_cover	Percentage ground cover within the releve that is covered by any stone greater than 10cm in diameter.	%
Wood_debris	Percentage ground cover within the releve that is covered any dead and decaying woody material.	%
TWI	Topographical wetness index.	
TPI	Topographical position index.	
Aspect		Degree
Northness	Calculated from Aspect; values of 1 = North, -1 = South, 0 = East or West.	Degree
Eastness	Calculated from Aspect.	Degree
Slope	Degrees from horizontal.	Degree
Solar	Potential solar radiation.	WH/m^2
% 2 mm	Proportion of total soil collected that is less than 2 mm diameter.	%
% 4 mm	Proportion of total soil collected that is 2-4 mm diameter.	%
% 8 mm	Proportion of total soil collected that is 4-8 mm diameter.	%
% >8 mm	Proportion of total soil collected that is greater than 8 mm diameter.	%
Sand	Proportion of sand found in soil by weight.	%
Clay	Proportion of clay found in soil by weight.	%
Silt	Proportion by weight (calculated as 100 - (%sand + %clay)).	%
Sand>1000	Percentage by weight of sand that is greater than 1000 ɥm diameter.	%
Sand>500	Percentage by weight of sand that is greater than 500 ɥm diameter.	%
Sand>250	Percentage by weight of sand that is greater than 250 ɥm diameter.	%
Sand>100	Percentage by weight of sand that is greater than 100 ɥm diameter.	%
Sand>53	Percentage by weight of sand that is greater than 53 ɥm diameter.	%
Sand<53	Percentage by weight of sand that is less than 53 ɥm diameter.	%
pH_H2O	pH of soil in ionised water.	
pH_CaCl2	pH of soil in ionised water with CaCl2	
Potassium	Miligrams per kg.	mg/kg
Magnesium	Miligrams per kg.	mg/kg
Phosphorous	Miligrams per kg.	mg/kg
Sodium	Miligrams per kg.	mg/kg
Calcium	Miligrams per kg.	mg/kg
Carbon	Percentage by weight.	%

Table S3. The 30 most commonly recorded species in Lapalala Wilderness Nature Reserve.

Species	**Frequency of occurrence**
Digitaria eriantha	134
Combretum apiculatum	128
Phyllanthus parvulus	126
Waltheria indica	121
Combretum molle	120
Commelina africana	120
Cyperus obtusiflorus	120
Dichrostachys cinerea	119
Grewia monticola	119
Schmidtia pappophoroides	117
Loudetia simplex	115
Solanum campylacanthum (invasive)	114
Pavonia transvaalensis	108
Sida cordifolia	107
Grewia caffra	102
Evolvulus alsinoides	99
Indigastrum costatum	99
Eragrostis rigidior	98
Chamaecrista mimosoides	94
Melinis repens	91
Panicum maximum	88
Tephrosia purpurea	87
Boscia albitrunca	85
Asparagus sp.	83
Combretum zeyheri	83
Lantana rugosa	83
Pellaea calomelanos	83
Diplorhynchus condylocarpon	82
Indigofera daleoides	80
Terminalia sericea	80

Table S4. The 355 species recorded during the study at Lapalala Wilderness Nature Reserve, organised by family.

Acanthaceae

- *Asystasia atriplicifolia* Bremek.
- *Barleria pretor*iensis C.B.Clarke
- *Blepharis saxatilis* Oberm.
- *Crabbea angustifolia* Nees
- *Dicliptera paniculata* (Forssk.) I.Darbysh.
- *Hypoestes forskaolii* (Vahl) R.Br.
- *Justicia divaricata* (Licht. ex Roem. & Schult.) T.Anderson
- *Justicia protracta* (Nees) T.Anderson
- *Ruellia patula* Jacq.
- *Thunbergia neglecta* Sond.

Agavaceae

- *Chlorophytum recurvifolium* (Baker) C.Archer & Kativu

Amaranthaceae

- *Pupalia lappacea* (L.) A.Juss.
- *Achyranthes aspera* L.*
- *Alternanthera pungens* Kunth*
- *Cyathula lanceolata* Schinz
- *Cyphocarpa angustifolia* (Moq.) Lopr.
- *Gomphrena celosioides* Mart.*
- *Hermbstaedtia fleckii* (Schinz) Baker & C.B.Clarke

Amaryllidaceae

- *Boophone disticha* (L.f.) Herb.

Anacardiaceae

- *Lannea discolor* (Sond.) Engl.
- *Ozoroa sphaerocarpa* R.Fern. & A.Fern.
- *Sclerocarya birrea* (A.Rich.) Hochst.
- *Searsia chirindensis* (Baker f.) Moffett
- *Searsia dentata* (Thunb.) F.A.Barkley
- *Searsia lancea* (L.f.) F.A.Barkley
- *Searsia pyroides* (Burch.) Moffett
- *Searsia zeyheri* (Sond.) Moffett

Annonaceae

- *Hexalobus monopetalus* (A.Rich.) Engl. & Diels

Apiaceae

- *Heteromorpha arborescens* (Spreng.) Cham. & Schltdl.

Apocynaceae

- *Asclepias burchellii* Schltr.
- *Carissa bispinosa* (L.) Desf. ex Brenan
- *Cryptolepis oblongifolia* (Meisn.) Schltr.
- *Diplorhynchus condylocarpon* (Mull.Arg.) Pichon

Orbea carnosa (Stent) Bruyns

Araliaceae

Cussonia spicata Thunb.

Asparagaceae

Asparagus sp.

Asphodelaceae

Bulbine abyssinica A.Rich.

Asteraceae

Berkheya zeyheri Oliv. & Hiern
Bidens pilosa L.*
Emilia transvaalensis (Bolus) C.Jeffrey
Felicia mossamedensis (Hiern) Mendonça
Felicia muricata (Thunb.) Nees
Gazania krebsiana Less.
Geigeria burkei Harv.
Helichrysum cerastioides DC.
Helichrysum stenopterum DC.
Hilliardiella elaeagnoides (DC.) Swelank. & J.C.Manning
Hirpicium bechuanense (S.Moore) Roessler
Mesogramma apiifolium DC.
Schistostephium crataegifolium (DC.) Fenzl ex Harv.
Senecio barbertonicus Klatt
Senecio erubescens Aiton
Senecio oxyriifolius DC.
Ursinia nana DC.

Boraginaceae

Cynoglossum hispidum Thunb.
Heliotropium ciliatum Kaplan
Heliotropium strigosum Willd.

Burseraceae

Commiphora edulis (Klotzsch) Engl.
Commiphora harveyi (Engl.) Engl.

Capparaceae

Boscia albitrunca (Burch.) Gilg & Gilg-Ben.
Boscia foetida Schinz

Celastraceae

Gymnosporia buxifolia (L.) Szyszyl.
Pleurostylia capensis (Turcz.) Loes.

Chrysobalanaceae

Parinari capensis Harv.

Cleomaceae

Cleome maculata (Sond.) Szyszyl.
Cleome monophylla L.

Cleome rubella Burch.

Colchicaceae

Gloriosa rigidifolia (Bredell) J.C.Manning & Vinn.

Combretaceae

Combretum apiculatum Sond.
Combretum hereroense Schinz
Combretum imberbe Wawra
Combretum molle R.Br. ex G.Don
Combretum nelsonii Dummer
Combretum zeyheri Sond.
Terminalia sericea Burch. ex DC.

Commelinaceae

Commelina africana L.
Commelina benghalensis L.
Commelina erecta L.
Cyanotis speciosa (L.f.) Hassk.

Convolvulaceae

Evolvulus alsinoides (L.) L.
Ipomoea bolusiana Schinz
Ipomoea crassipes Hook.
Ipomoea gracilisepala Rendle
Ipomoea magnusiana Schinz
Ipomoea obscura (L.) Ker Gawl.
Ipomoea ommanneyi Rendle
Ipomoea papilio Hallier f.
Merremia pinnata (Hochst. ex Choisy) Hallier f.
Seddera capensis (E.Mey. ex Choisy) Hallier f.
Xenostegia tridentata (L.) D.F.Austin & Staples

Crassulaceae

Crassula capitella Thunb.
Crassula lanceolata (Eckl. & Zeyh.).
Kalanchoe paniculata Harv.

Cucurbitaceae

Coccinia sessilifolia (Sond.) Cogn.
Kedrostis foetidissima (Jacq.) Cogn.

Cyperaceae

Ascolepis capensis (Kunth) Ridl.
Bulbostylis burchellii (Ficalho & Hiern) C.B.Clarke
Bulbostylis hispidula (Vahl) R.W.Haines
Cyperus esculentus L.
Cyperus obtusiflorus Vahl
Cyperus rupestris Kunth
Fuirena pubescens (Poir.) Kunth

*Kyllinga a*lba Nees

Schoenoplectus corymbosus (Roth ex Roem. & Schult.) J.Raynal

Dichapetalaceae

Dichapetalum cymosum (Hook.) Engl.

Ebenaceae

Euclea crispa (Thunb.) Gurke

Euclea divinorum Hiern

Euclea linearis Zeyh. ex Hiern

Euclea natalensis A.DC.

Euclea undulata Thunb.

Euphorbiaceae

Croton gratissimus Burch.

Dalechampia capensis A.Spreng.

Euphorbia neopolycnemoides Pax & K.Hoffm.

Euphorbia schinzii Pax

Tragia dioica Sond.

Fabaceae

Burkea africana Hook.

Chamaecrista mimosoides (L.) Greene

Crotalaria schinzii Baker f.

Dichrostachys cinerea (L.) Wight & Arn.

Elephantorrhiza burkei Benth.

Indigastrum costatum (Guill. & Perr.) Schrire

Indigofera bainesii Baker

Indigofera daleoides Benth. ex Harv.

Indigofera filipes Benth. ex Harv.

Indigofera heterotricha DC.

Indigofera ingrata N.E.Br.

Indigofera melanadenia Benth. ex Harv.

Lablab purpureus (L.) Sweet

Mundulea sericea (Willd.) A.Chev.

Neorautanenia ficifolia (Benth.) C.A.Sm.

Peltophorum africanum Sond.

Pterocarpus rotundifolius (Sond.) Druce

Schotia brachypetala Sond.

Senegalia burkei (Benth.) Kyal. & Boatwr.

Senegalia nigrescens (Oliv.) P.J.H.Hurter

Sphenostylis angustifolia Sond.

Tephrosia purpurea (L.) Pers.

Tylosema fassoglense (Schweinf.) Torre & Hillc.

Vachellia hebeclada (DC.) Kyal. & Boatwr.

Vachellia nilotica (L.) P.J.H.Hurter & Mabb.

Vachellia sieberiana (DC.) Kyal. & Boatwr.

Vachellia tortilis (Forssk.) Galasso & Banfi
Zornia milneana Mohlenbr.

Geraniaceae

Monsonia angustifolia E.Mey. ex A.Rich.

Gisekiaceae

Gisekia africana (Lour.) Kuntze

Heteropyxidaceae

Heteropyxis natalensis Harv.

Hyacinthaceae

Albuca seineri (Engl. & K.Krause) J.C.Manning & Goldblatt
Dipcadi marlothii Engl.
Drimia sp.
Ledebouria cooperi (Hook.f.) Jessop
Ledebouria luteola Jessop
Ledebouria marginata (Baker) Jessop

Hypoxidaceae

Hypoxis iridifolia Baker

Iridaceae

Afrosolen sandersonii (Baker) Goldblatt & J.C.Manning
Gladiolus dalenii Van Geel
Gladiolus permeabilis D.Delaroche

Kirkiaceae

Kirkia acuminata Oliv.

Lamiaceae

Acrotome hispida Benth.
Clerodendrum ternatum Schinz
Hemizygia canescens (Gurke) M.Ashby
Leonotis leonurus (L.) R.Br.
Ocimum filamentosum Forssk.
Satureja biflora (Buch.-Ham. ex D.Don) Briq.
Teucrium trifidum Retz.
Vitex obovata E.Mey.
Vitex pooara Corbishley
Vitex rehmannii Gurke

Limeaceae

Limeum fenestratum (Fenzl) Heimerl
Limeum viscosum (J.Gay) Fenzl

Linderniaceae

Lindernia sp.

Lobeliaceae

Monopsis decipiens (Sond.) Thulin

Loganiaceae

Strychnos madagascariensis Poir.

Malpighiaceae

Sphedamnocarpus pruriens (A.Juss.) Szyszyl.

Malvaceae

Cienfuegosia digitata Cav.

Corchorus aspleniifolius Burch.

Dombeya rotundifolia (Hochst.) Planch.

Grewia caffra Meisn.

Grewia flava DC.

Grewia flavescens Juss.

*Grewia mont*icola Sond.

Hermannia quartiniana A.Rich.

Hibiscus calyphyllus Cav.

Hibiscus lunariifolius Willd.

Hibiscus micranthus L.f.

Hibiscus nigricaulis Baker f.

Hibiscus physaloides Guill. & Perr.

Hibiscus sidiformis Baill.

Hibiscus trionum L.*

Melhania acuminata Mast.

Melhania prostrata DC.

Pavonia senegalensis (Cav.) Leistner

Pavonia transvaalensis (Ulbr.) A.Meeuse

Sida cordifolia L.

Sida dregei Burtt Davy

Triumfetta sonderi Ficalho & Hiern

Waltheria indica L.

Meliaceae

Turraea obtusifolia Hochst.

Moraceae

Ficus burkei (Miq.) Miq.

Ficus thonningii Blume

Myricaceae

Morella serrata (Lam.) Killick

Nyctaginaceae

Boerhavia repens L.

Ochnaceae

Ochna pulchra Hook.f.

Ochna serrulata (Hochst.) Walp.

Olacaceae

Ximenia americana L.

Ximenia caffra Sond.

Oxalidaceae

Oxalis corniculata L.*

Oxalis obliquifolia Steud. ex A.Rich.

Pedaliaceae

Ceratotheca triloba (Bernh.) Hook.f.
Dicerocaryum eriocarpum (Decne.) Abels
Harpagophytum procumbens Burch. ex Meisn.

Phrymaceae

Mimulus gracilis R.Br.

Phyllanthaceae

Bridelia mollis Hutch.
Phyllanthus parvulus Sond.
Pseudolachnostylis maprouneifolia Pax

Poaceae

Andropogon chinensis (Nees) Merr.
Andropogon eucomus Nees
Andropogon huillensis Rendle
Anthephora pubescens Nees
Aristida adscensionis L.
Aristida congesta Roem. & Schult.
Aristida diffusa Trin.
Aristida junciformis Trin. & Rupr.
Aristida stipitata Hack.
Arundinella nepalensis Trin.
Bothriochloa radicans (Lehm.) A.Camus
Brachiaria deflexa (Schumach.) C.E.Hubb. ex Robyns
Brachiaria eruciformis (Sm.) Griseb.
Brachiaria serrata (Thunb.) Stapf
Cenchrus ciliaris L.
Chloris virgata Sw.
Chrysopogon serrulatus Trin.
Cymbopogon pospischilii (K.Schum.) C.E.Hubb.
Cynodon dactylon (L.) Pers.
Dichanthium annulatum (Forssk.) Stapf
Digitaria eriantha Steud.
Digitaria monodactyla (Nees) Stapf
Digitaria sanguinalis (L.) Scop.
Digitaria ternata (A.Rich.) Stapf
Diheteropogon amplectens (Nees) Clayton
Elionurus muticus (Spreng.) Kunth
Enneapogon cenchroides (Licht. ex Roem. & Schult.) C.E.Hubb.
Enteropogon macrostachyus (Hochst. ex A.Rich.) Munro ex Benth.
Eragrostis capensis (Thunb.) Trin.
Eragrostis gummiflua Nees
Eragrostis heteromera Stapf

Eragrostis inamoena K.Schum.
Eragrostis nindensis Ficalho & Hiern
Eragrostis patentipilosa Hack.
Eragrostis racemosa (Thunb.) Steud.
Eragrostis rigidior Pilg.
Eragrostis superba Peyr.
Eustachys paspaloides (Vahl) Lanza & Mattei
Helictotrichon turgidulum (Stapf) Schweick.
Heteropogon contortus (L.) Roem. & Schult.
Hyperthelia dissoluta (Nees ex Steud.) Clayton
Loudetia simplex (Nees) C.E.Hubb.
Melinis nerviglumis (Franch.) Zizka
Melinis repens (Willd.) Zizka
Microchloa caffra Nees
Panicum deustum Thunb.
Panicum maximum Jacq.
Pennisetum thunbergii Kunth
Perotis patens Gand.
Pogonarthria squarrosa (Roem. & Schult.) Pilg.
Sporobolus ioclados (Trin.) Nees
Schmidtia pappophoroides Steud.
Setaria sphacelata (Schumach.) Stapf & C.E.Hubb. ex M.B.Moss
Sorghum halepense (L.) Pers.*
Sporobolus festivus Hochst. ex A.Rich.
Sporobolus panicoides A.Rich.
Sporobolus stapfianus Gand.
Themeda triandra Forssk.
Tragus berteronianus Schult.
Tricholaena monachne (Trin.) Stapf & C.E.Hubb.
Trichoneura grandiglumis (Nees) Ekman
Urelytrum agropyroides (Hack.) Hack.
Urochloa mosambicensis (Hack.) Dandy
Urochloa oligotricha (Fig. & De Not.) Henrard
Urochloa panicoides P.Beauv.

Polygalaceae

Polygala amatymbica Eckl. & Zeyh.
Polygala hottentotta C.Presl

Polygonaceae

Oxygonum alatum Burch.
Oxygonum dregeanum Meisn.
Oxygonum sinuatum (Hochst. & Steud. ex Meisn.) Dammer

Portulacaceae

Portulaca quadrifida L.

Proteaceae
Faurea saligna Harv.
Pteridaceae
Pellaea calomelanos (Sw.) Link
Rhamnaceae
Berchemia discolor (Klotzsch) Hemsl.
Ziziphus mucronata Willd.
Rubiaceae
Afrocanthium gilfillanii (N.E.Br.) Lantz
Agathisanthemum bojeri Klotzsch
Coptosperma supra-axillare (Hemsl.) Degreef
Cordylostigma virgatum (Willd.) Groeninckx & Dessein
Fadogia homblei De Wild.
Gardenia volkensii K.Schum.
Pavetta capensis (Houtt.) Bremek.
Psydrax livida (Hiern) Bridson
Spermacoce senensis (Klotzsch) Hiern
Vangueria dryadum S.Moore
Vangueria parvifolia Sond.
Ruscaceae
Eriospermum flagelliforme (Baker) J.C.Manning
Eriospermum porphyrovalve Baker
Sansevieria sp.
Salicaceae
Dovyalis zeyheri (Sond.) Warb.
Santalaceae
Thesium utile A.W.Hill
Sapotaceae
Englerophytum magalismontanum (Sond.) T.D.Penn.
Solanaceae
Datura ferox L.*
Solanum campylacanthum Hochst. ex A.Rich.
Solanum catombelense Peyr.
Stilbaceae
Nuxia oppositifolia (Hochst.) Benth.
Talinaceae
Talinum arnotii Hook.f.
Talinum caffrum (Thunb.) Eckl. & Zeyh.
Thymelaeaceae
Gnidia sericocephala (Meisn.) Gilg ex Engl.
Turneraceae
Afroqueta capensis (Harv.) Thulin & Razafim.
Urticaceae

Pouzolzia mixta Solms

Vahliaceae

Vahlia capensis (L.f.) Thunb.

Velloziaceae

Xerophyta humilis (Baker) T.Durand & Schinz

Xerophyta retinervis Baker

Verbenaceae

Chascanum hederaceum (Sond.) Moldenke

Chascanum pinnatifidum (L.f.) E.Mey.

Lantana rugosa Thunb.

Lippia rehmannii H.Pearson

Priva adhaerens (Forssk.) Chiov.

Vitaceae

Cyphostemma sandersonii (Harv.) Desc.

Zygophyllaceae

Tribulus terrestris L.

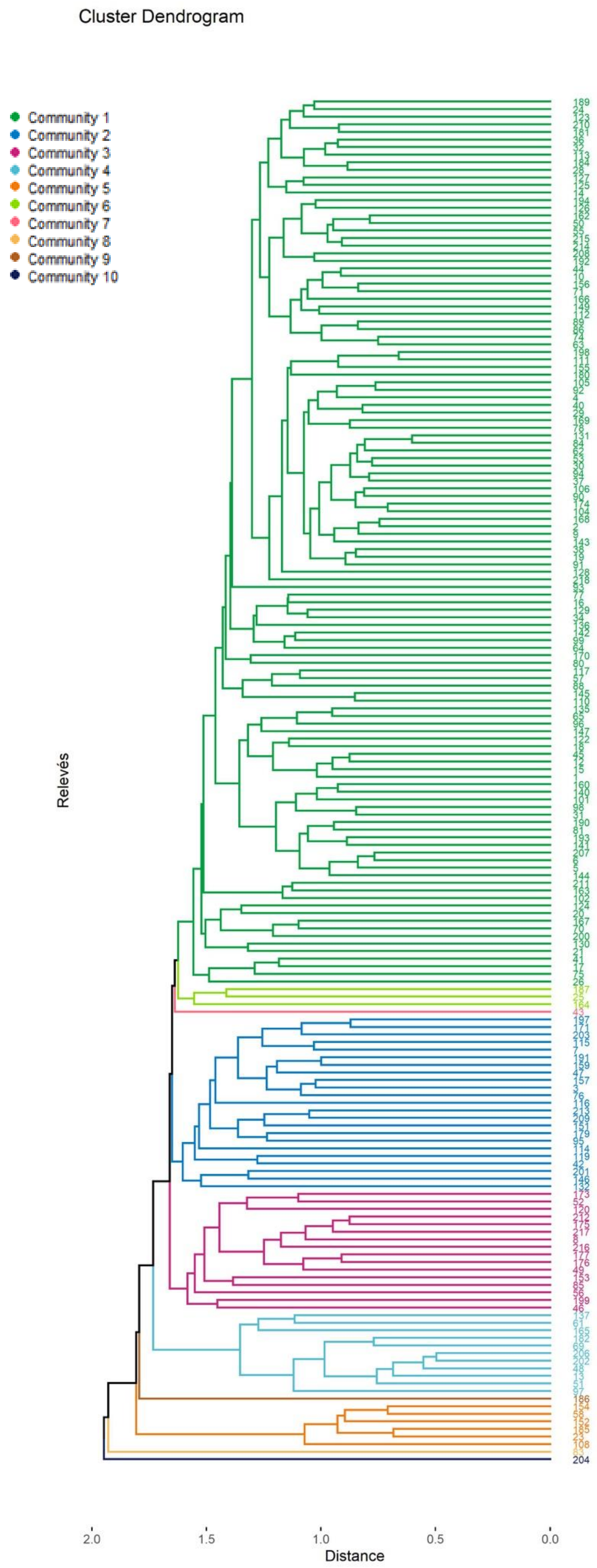

Figure S3. Dendrogram showing the relatedness of all relevés within the 10 communities.

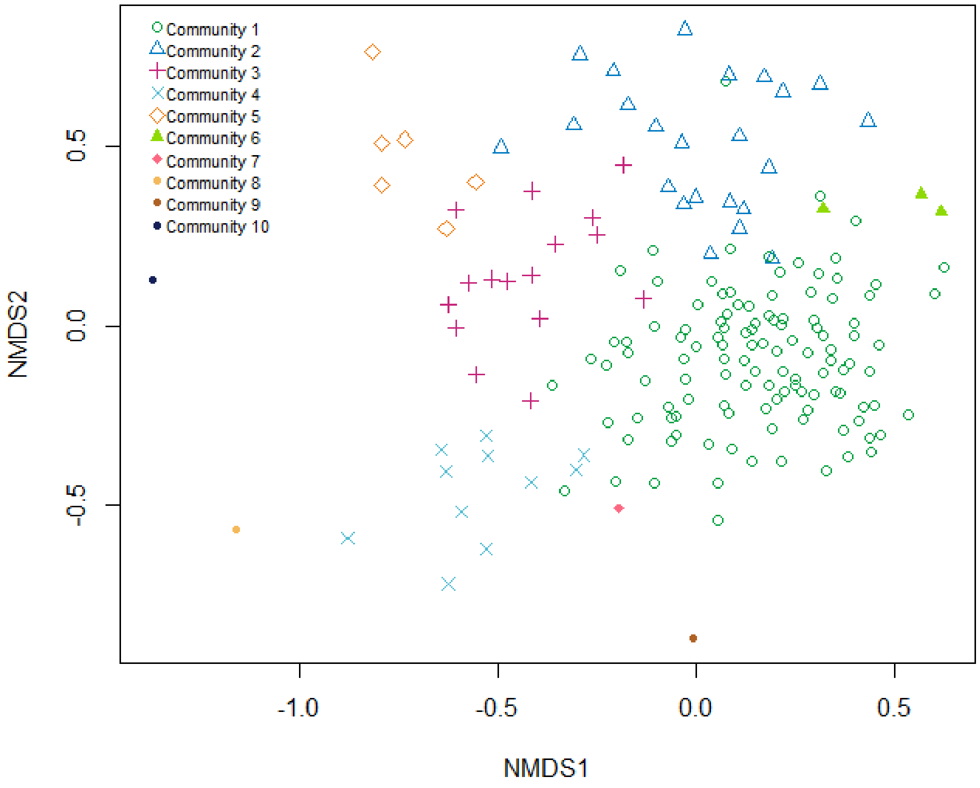

Figure S4. NMDS showing relatedness of releves sampled at Lapalala Wilderness Nature reserve.

Table S5. Diagnostic, prominent and dominant species of the 10 communities identified at Lapalala Wilderness Nature Reserve.

Vegetation Unit	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Number of Releves	117	23	16	11	6	3	1	1	1	1
Total number of species	281	217	168	116	72	74	27	11	14	18
Mean species per plot ± SD	50 ± 12	50 ± 12	40 ± 10	29 ± 8	28 ± 7	34 ± 10				
Speices richness estimation (Chao ± SE)	313 ± 12	312 ± 30	221 ± 19	169 ± 20	98 ± 12	134 ± 24				
Diagnostic species (calculated for units 1 - 5 only)	*Combretum molle* *Diplorhynchus condylocarpon* *Loudetia simplex* *Schmidtia pappophoroides* *Elephantorrhiza burkei* *Harpagophytum procumbens* *Lannea discolor* *Pseudolachnostylis maprouneifolia* *Pterocarpus rotundifolius* *Xerophyta retinervis*	*Enneapogon cenchroides* *Enteropogon macrostachyus* *Ximenia americana* *Berchemia discolor* *Chascanum hederaceum* *Dombeya rotundifolia* *Grewia flava* *Heteropogon contortus* *Heteropyxis natalensis* *Panicum deustum* *Ruellia patula* *Senegalia nigrescens* *Ziziphus mucronata* *Chrysopogon serrulatus* *Clerodendrum ternatum* *Crabbea angustifolia* *Cymbopogon pospischilii* *Dichrostachys cinerea* *Grewia caffra* *Grewia monticola* *Gymnosporia buxifolia* *Lablab purpureus* *Lantana rugosa* *Melhania prostrata* *Vachellia tortilis*	*Aristida diffusa* *Digitaria eriantha* *Pogonarthria squarrosa* *Eragrostis rigidior* *Euclea natalensis* *Fadogia homblei* *Limeum fenestratum* *Terminalia sericea*	*Cordylostigma virgata* *Eragrostis gummiflua* *Chamaecrista mimosoides* *Helichrysum cerastioides* *Indigastrum costatum* *Sporobolus stapfianus* *Agathisanthemum bojeri* *Cyperus esculentus* *Eragrostis racemosa* *Eriospermum porphyrovalve* *Faurea saligna* *Oxalis obliquifolia*	*Acanthospermum hispidum* *Cynodon dactylon* *Eragrostis patentipilosa* *Gomphrena celosioides* *Portulaca quadrifida* *Schistostephium crataegifolium* *Sida cordifolia* *Solanum campylacanthum* *Boerhavia repens* *Cleome monophylla* *Dicerocaryum eriocarpum* *Sporobolus festivus* *Tribulus terrestris* *Alternanthera pungens* *Bulbostylis hispidula* *Datura ferox* *Gardenia volkensii* *Gisekia africana* *Hirpicium bechuanense* *Melinis nerviglumis* *Monsonia angustifolia* *Oxygonum sinuatum* *Satureja biflora* *Seddera capensis* *Tragus berteronianus* *Urochloa panicoides* *Waltheria indica*					
Prominent species (species with greater cover within the unit than teh sum of the cover in all other units) with greater than 1% cover, ordered decending by cover	*Diplorhynchus condylocarpon* *Croton gratissimus* *Loudetia simplex* *Pseudolachnostylis maprouneifolia* *Lannea discolor* *Elephantorrhiza burkei*	*Heteropogon contortus* *Senegalia nigrescens* *Enneapogon cenchroides* *Vachellia tortilis* *Panicum deustum* *Grewia flava* *Enteropogon macrostachyus* *Ximenia americana* *Heteropyxis natalensis* *Cenchrus ciliaris* *Sclerocarya birrea* *Berchemia discolor* *Chrysopogon serrulatus* *Tylosema fassoglense* *Chascanum hederaceum* *Ipomoea magnusiana* *Ruellia patula* *Eragrostis superba* *Lablab purpureus*	*Terminalia sericea* *Aristida diffusa* *Andropogon chinensis* *Xerophyta humilis* *Fadogia homblei* *Pogonarthria squarrosa* *Limeum fenestratum*	*Eragrostis gummiflua* *Burkea africana* *Geigeria burkei* *Sporobolus stapfianus* *Faurea saligna* *Afrosolen sandersonii* *Eriospermum porphyrovalve* *Oxalis obliquifolia* *Urochloa mosambicensis*	*Cynodon dactylon* *Schistostephium crataegifolium* *Tragus berteronianus* *Eragrostis patentipilosa* *Portulaca quadrifida* *Bulbostylis hispidula* *Gomphrena celosioides* *Monsonia angustifolia* *Cleome monophylla* *Gisekia africana* *Acanthospermum hispidum* *Tribulus terrestris* *Satureja biflora* *Hibiscus physaloides* *Boerhavia repens* *Felicia muricata* *Alternanthera pungens* *Oxygonum sinuatum* *Sphenostylis angustifolia* *Hibiscus nigricaulis* *Seddera capensis* *Datura ferox* *Hirpicium bechuanense* *Melinis nerviglumis*	*Grewia monticola* *Grewia caffra* *Bridelia mollis* *Kirkia acuminata* *Strychnos madagascariensis* *Pavonia transvaalensis* *Vachellia sieberiana* *Euphorbia neopolycnemoides* *Commelina erecta* *Senegalia burkei* *Gloriosa rigidifolia* *Thunbergia neglecta* *Aristida stipitata* *Clerodendrum ternatum* *Vitex rehmannii* *Harpagophytum procumbens* *Acacia fleckii* *Coccinia sessilifolia* *Helictotrichon turgidulum* *Vachellia nilotica*	*Euclea linearis* *Ochna serrulata* *Microchloa caffra* *Cordylostigma virgata* *Hermannia quartiniana* *Limeum viscosum* *Xenostegia tridentata* *Dipcadi marlothii* *Brachiaria serrata* *Polygala amatymbica*	*Cymbopogon pospischilii* *Dicerocaryum eriocarpum* *Senecio barbertonicus*	*Euclea natalensis* *Vitex obovata* *Zornia milneana* *Indigofera daleoides* *Felicia mossamedensis* *Ochna pulchra*	*Andropogon eucomus* *Setaria sphacelata* *Eragrostis heteromera* *Andropogon huillensis* *Arundinella nepalensis* *Hypericum lalandii* *Monopsis decipiens* *Senecio erubescens* *Urochloa panicoides* *Cyperus esculentus* *Fuirena pubescens* *Hilliardiella elaeagnoides* *Gladiolus dalenii* *Oxalis corniculata*
Dominent Candidate Index species (Index cutoff is 0.3, ordered descending). Needs more than 1 releve to calculate - for units with only 1 releve, the top 5 species with most cover are shown	*Schmidtia pappophoroides* *Combretum molle* *Loudetia simplex* *Combretum apiculatum* *Digitaria eriantha* *Pavonia transvaalensis* *Commelina africana* *Cyperus obtusiflorus* *Grewia monticola* *Phyllanthus parvulus* *Diplorhynchus condylocarpon* *Indigastrum costatum* *Waltheria indica* *Solanum campylacanthum* *Lannea discolor* *Grewia caffra* *Pellaea calomelanos* *Dichrostachys cinerea*	*Dichrostachys cinerea* *Lantana rugosa* *Grewia monticola* *Aristida congesta* *Solanum campylacanthum* *Melhania prostrata* *Heteropogon contortus* *Waltheria indica* *Grewia caffra* *Combretum apiculatum* *Commelina africana* *Eragrostis rigidior* *Evolvulus alsinoides* *Phyllanthus parvulus* *Enneapogon cenchroides* *Digitaria eriantha* *Ximenia americana* *Melinis repens* *Tragus berteronianus* *Schistostephium crataegifolium* *Tephrosia purpurea* *Senegalia nigrescens*	*Digitaria eriantha* *Terminalia sericea* *Dichrostachys cinerea* *Eragrostis rigidior* *Aristida diffusa* *Cyperus obtusiflorus* *Sida cordifolia* *Waltheria indica* *Panicum maximum* *Melinis repens* *Phyllanthus parvulus* *Grewia caffra* *Euclea natalensis* *Evolvulus alsinoides* *Peltophorum africanum*	*Eragrostis gummiflua* *Terminalia sericea* *Indigastrum costatum* *Chamaecrista mimosoides* *Phyllanthus parvulus* *Sida cordifolia* *Agathisanthemum bojeri* *Cordylostigma virgata* *Combretum zeyheri*	*Cynodon dactylon* *Schistostephium crataegifolium* *Solanum campylacanthum* *Dichrostachys cinerea* *Sida cordifolia* *Portulaca quadrifida* *Digitaria eriantha* *Eragrostis patentipilosa* *Waltheria indica* *Gardenia volkensii* *Gomphrena celosioides* *Cyperus obtusiflorus*	*Combretum apiculatum* *Grewia monticola* *Dichrostachys cinerea* *Schmidtia pappophoroides* *Pavonia transvaalensis* *Eragrostis rigidior* *Grewia caffra* *Bridelia mollis* *Combretum zeyheri* *Sida cordifolia* *Kirkia acuminata* *Strychnos madagascariensis* *Pterocarpus rotundifolius* *Combretum molle* *Ziziphus mucronata* *Evolvulus alsinoides* *Euclea natalensis* *Euphorbia neopolycnemoides* *Melhania prostrata* *Panicum deustum* *Schistostephium crataegifolium*	*Euclea linearis* *Agathisanthemum bojeri* *Digitaria eriantha* *Aristida congesta* *Eragrostis gummiflua*	*Cymbopogon pospischilii* *Eragrostis gummiflua* *Aristida congesta* *Setaria sphacelata* *Agathisanthemum bojeri*	*Terminalia sericea* *Phyllanthus parvulus* *Combretum apiculatum* *Chamaecrista mimosoides* *Cyperus obtusiflorus*	*Andropogon eucomus* *Setaria sphacelata* *Eragrostis heteromera* *Andropogon huillensis* *Arundinella nepalensis*

Table S6. Sorted phytosociological table for the sub-communities of Community 1 *Combretum molle-Schmidtia pappophoroides* woodland of Lapalala Wilderness Nature Reserve. Only the four sub-communities which had more than one sampled releve are shown here. The body of the table shows species cover (%) per relevé. Significance indicated by asterisks, where $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***).

		1	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
		1	2	4	5	6	9	10	12	14	15	18	19	20	24	28	29	30	31	32	36	37	38	40	41	44	45	50	53	55	62	63	64	70	71	74	77	78	80	81	84	85
Gisekia africana	*	2	2				2	2	2		2		2		2		2		2		2	2	2	2		2		2	2	2	2	2			2	2	2				2	
Grewia monticola	**	3	7	3	4		3	3	4	2	4	5		4		2	2	4	4	2	2	3		5	3	2	2	3	3	2	5	17	3	5	4	2	2	2	7		4	4
Indigastrum costatum	**	2	2	2	2	2	2	2	2	2	2		2	2	2	2	2	2	2		2	2		2	2	2	2	2	2	4						2	2	2		2	2	2
Ipomoea magnusiana	*			2		2	2	2							2		2	2		2	2			2	2			2	2		2	2			2	2					2	
Melhania prostrata	***						2	2		2					4	2	2				2			2			2	2		2	2	2	2	2	2	2		2	11		2	
Tephrosia purpurea	*	2						2		2	2	2	2		2		2	2		2	2		2	2	2	2	2	2		2	2	2			2	2		2	2		2	2
Xenostegia tridentata	*	2		2	2	2	2	2	2	2						2		2	2	2	2	2	2	2		2	2		2		2	2			2	2					2	2
Asclepias burchellii	***																							2		2																
Asparagus sp	*			2				2	2					2	2	2	2	2		2		2	2	3			2	2	2	2		2	2	3	3	2		2	2		2	2
Brachiaria deflexa	**																																									
Chlorophytum recurvifolium	**																													2			2									
Cienfuegosia digitata	**																																									
Senecio barbertonicus	**																																									
Andropogon chinensis	**	3		2	2											4			2					2	2											2					2	2
Blepharis saxatilis	*													2								2		2																		
Chrysopogon serrulatus	*						3																			2																
Eragrostis racemosa	*																																			2						2
Euclea linearis	*																								3	2																
Hemizygia canescens	*							2		2																		2														2
Heteropogon contortus	***					3					2		3					2				3		6		2		2	2	2			2	2		2			2	3		
Lannea discolor	*		2					7	2	5			3		2	6	10	4		3	8	12	2	2	12	5		2	5	6		4	21	6			2	2		4	2	2
Themeda triandra	**													4																												
Trichoneura grandiglumis	*																					2		2											2							
Aristida stipitata	*				2		2												2						3			2														
Eragrostis rigidior	*	6	2		6	3	2	2				2	2			3	2					3	2	5		2	2	7				3		2	3	6	2		2			8
Grewia caffra	**	4		6							2	3	3	2	3	3	4		2		6	2	2	2	3	3	2	5		8		8		12	12		5		3	2		3
Indigofera ingrata	*																2													2								2		2		
Limeum fenestratum	*						2	2	2				2						2	2	2					2	2								2	2						
Nuxia oppositifolia	**																																									
Senegalia burkei	*																																									
Sida cordifolia	*	3	2						3		2	2	2		2		2			2	2		2		2					3			2	6			4	2	2	2		
Sporobolus ioclados	***																																									

Table S5. Continued

		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		86	89	90	91	92	94	98	99	101	105	106	112	113	122	123	124	125	126	127	128	131	140	143	144	149	153	156	160	162	164	166	167
Gisekia africana	*	2	2	2	2	2	2						2					2		2		2		2	2	2		2	2			2	
Grewia monticola	**	2	2	3	3			2		2	3	7	16	5	4			2	5	5	8	3	5	2		12			2	5	2	2	3
Indigastrum costatum	**			2	2		2	2	2	2	4	2	2	2	2	3	2	2	2	2			2			2			2	2	2	2	2
Ipomoea magnusiana	*	2	2										2				2					2					2			2		2	2
Melhania prostrata	***				2		2		2	2			2	2	2	4			2		2	2	2	2	2	2	2	2		2	2	2	4
Tephrosia purpurea	*	2	2						2		2	2	2	2		2	2		2		2	2			2	2	2		2	2	2	2	2
Xenostegia tridentata	*	2	2	2	2								2	2								2		2	3	2		2				2	
Asclepias burchellii	***													2		2												2					
Asparagus sp	*	2	2		2	2			2	2	5	2	2	4	2	2					2			2		2						2	
Brachiaria deflexa	**																																
Chlorophytum recurvifolium	**																																
Cienfuegosia digitata	**																																
Senecio barbertonicus	**																																
Andropogon chinensis	**						2				2						2					2		2									
Blepharis saxatilis	*			2																										2			
Chrysopogon serrulatus	*																		2													2	
Eragrostis racemosa	*													2																			
Euclea linearis	*				2																												
Hemizygia canescens	*												2																				
Heteropogon contortus	***				2	2	2				2			3	10	2			2			2				3				2			2
Lannea discolor	*	2				2	12		2	9	2	4	2	5		10	2		6	7			6	14		2		2		15		2	
Themeda triandra	**														2						2												
Trichoneura grandiglumis	*																																
Aristida stipitata	*								2																2				2	2			
Eragrostis rigidior	*	6			2	3						2	5							3	3	2			4	3	2	2			2	2	2
Grewia caffra	**		2		3	2	2		2		2	2	4	2		2	2		3		3	2					3	3		6	4		35
Indigofera ingrata	*						2	2		2							2						2										
Limeum fenestratum	*	2	2		2								2						2			2		2	2			2					
Nuxia oppositifolia	**																3																
Senegalia burkei	*																																
Sida cordifolia	*	2			2	2	2	2	2	4	2		2			4		2		2	2		2			2	2		4	2	25		2
Sporobolus ioclados	***																																

Table S6. Continued

		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
		168	169	170	181	184	189	190	192	194	200	207	208	210	214	215	218	16	21	34	57	65	88	96	117	129	135	136	142	147	155	198
Gisekia africana	*				2	2		2									2															
Grewia monticola	**	5	2	2	2	3		2	4	4		2	3	4	4		3	8	2	7		2		2		4			5	7	2	2
Indigastrum costatum	**	2	2	2	2	2	2	2	2	2	2	2	2	2		3	2	2				2		2					2			
Ipomoea magnusiana	*	2				2	2		2		2			2	2	2																
Melhania prostrata	***	2		2			2	2	2	2	2		2	2	2	2	2															
Tephrosia purpurea	*	2		2	2	2		4	2		2		2	2	2		2	2		2						2						
Xenostegia tridentata	*	2	2				2		4			2				2	2															
Asclepias burchellii	***																	2	2	4		2	2	2				2		4	4	2
Asparagus sp	*	2	2		2	2					2				2	2		4	2		6	2			2	4		4	4	2	4	2
Brachiaria deflexa	**																	2	2	2						2					2	
Chlorophytum recurvifolium	**																					2	2				2			2	2	
Cienfuegosia digitata	**																					2	2				2	2	2	2	2	2
Senecio barbertonicus	**											2							2		2								2		2	2
Andropogon chinensis	**	2				6	2		6	2	3		4		3	5										2		2				
Blepharis saxatilis	*												2																			
Chrysopogon serrulatus	*												4																			
Eragrostis racemosa	*															2																
Euclea linearis	*							2															6		2							
Hemizygia canescens	*											2	2			2																
Heteropogon contortus	***			4	2			3	2	2	3	2	2	2	2	4				2		2		2			2	2	2			
Lannea discolor	*	2	3	2		5	3		3	14		2				8	7	5	2					8		4	13		2	2	2	2
Themeda triandra	**			2																												
Trichoneura grandiglumis	*											2					2															
Aristida stipitata	*																	2	2	2	2	2	2	2	2		2		2	2	2	2
Eragrostis rigidior	*	2	2	2						2		2					2	2	3		2			2			3	3	3	2		2
Grewia caffra	**	2	2		11		7	2	4	3	5		6	4	3	2		8			11			2	5					2		
Indigofera ingrata	*																	2		2		2	2			2			2			
Limeum fenestratum	*	2																											2			
Nuxia oppositifolia	**																															
Senegalia burkei	*																															
Sida cordifolia	*	2			2	2		2	2					2	2			2	2	2	2	2	4	2	2	4	2	4	2	2	2	
Sporobolus ioclados	***																															

Table S5. Continued

		3	3	3	3	3	3	4	4	4
		102	104	163	174	193	211	110	111	145
Gisekia africana	*									
Grewia monticola	**					3				
Indigastrum costatum	**			2		2	2			
Ipomoea magnusiana	*									
Melhania prostrata	***									
Tephrosia purpurea	*					2				
Xenostegia tridentata	*									
Asclepias burchellii	***									
Asparagus sp	*									
Brachiaria deflexa	**									
Chlorophytum recurvifolium	**									
Cienfuegosia digitata	**									
Senecio barbertonicus	**									
Andropogon chinensis	**	26	23	20	6	2	21			
Blepharis saxatilis	*	2		2						
Chrysopogon serrulatus	*	11	3	2						
Eragrostis racemosa	*					2	2			
Euclea linearis	*			14	3		2			
Hemizygia canescens	*		2	2						
Heteropogon contortus	***	2	2	14	3	2	6			
Lannea discolor	*	10	12	4	11	2	7			
Themeda triandra	**		2	2	2	2	6		2	
Trichoneura grandiglumis	*			2		2	2			
Aristida stipitata	*			2				4	2	2
Eragrostis rigidior	*		2					5	2	2
Grewia caffra	**					2	2	5	2	7
Indigofera ingrata	*							2	2	
Limeum fenestratum	*							2		2
Nuxia oppositifolia	**							9		9
Senegalia burkei	*								2	
Sida cordifolia	*							4	2	2
Sporobolus ioclados	***							2		2

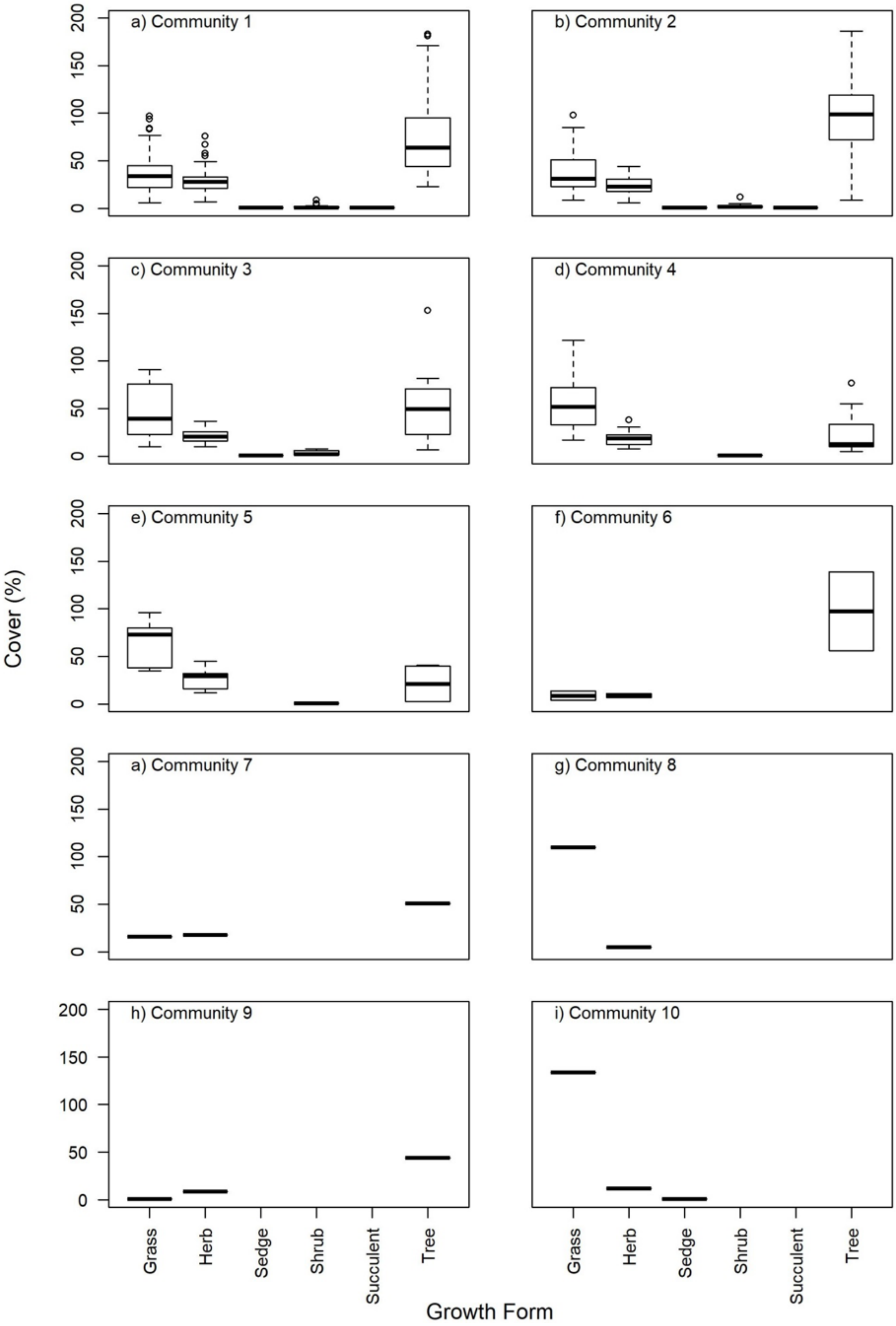

Figure S5. Average cover for each growth form within each of the ten terrestrial vegetation units. Thick lines indicate median values, boxes interquartile ranges, whiskers ranges, and empty symbols outliers.

Appendix C: Mapping

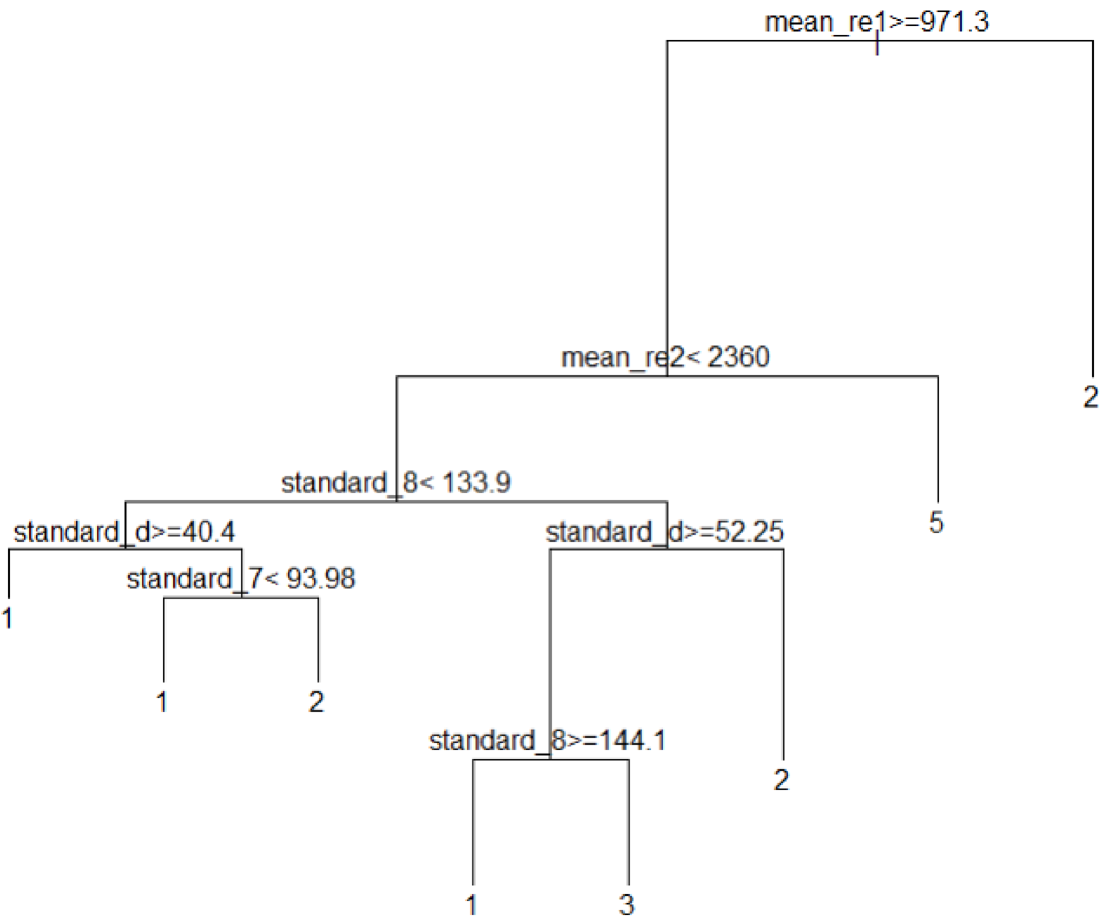

Figure S2. CART decision tree for classification of the vegetation of Lapalala Wilderness Nature Reserve, where mean_re1 = the mean value for red edge band 1, mean re2 = mean average for red edge band 2, standard_8 = standard deviation of the red band, standard_d = the standard deviation of the short wave infrared 2 band (SWIR2) and standard_7 = standard deviation of red edge 3 band (RE3). Numbers represent the community number.

Landscape images of Lapalala Wilderness Nature Reserve.

Landscape images of Lapalala Wilderness Nature Reserve.

Chapter 3: General Conclusion

Vegetation classifications distinguish plant communities present within an area, forming an objective basis for vegetation management and a baseline for future studies. In this study, a vegetation classification identified eleven plant communities within Lapalala Wilderness Nature Reserve (LWNR), consisting of one riparian community, two widespread communities and eight smaller communities interspersed between them. The environmental variables analysed in this study could not clearly distinguish the majority of the communities. However, of all the environmental variables examined, soil-based variables differed most between communities.

The Waterberg area is an important conservation region (Waterberg District Municipality, 2010; Desmet et al., 2013), and being able to map the vegetation of the entire Waterberg from remotely sensed data would be a potentially powerful conservation tool. As a result, the ability of the model created in this study to be extrapolated to the area immediately surrounding LWNR was briefly investigated. LWNR acquired a new piece of land after the commencement of this study and this new part of the reserve, along with the surrounding areas, was mapped using the model developed for the original extent of LWNR (including the same satellite imagery and CART rulesets; Figure 26). Extending the mapping area reduced the relative cover of Communities 1, 3 and 5 and increased the cover of Community 2. Ground truthing data (collected March 2021 by independent observers) indicates that overall accuracy of this map is greatly reduced (from 70 % in the original extent of LWNR, to 30 % in the newly acquired portion of LWNR). Therefore, even within a relatively small portion of the Waterberg, extrapolating classifications based solely on remotely sensed data is unlikely to provide accurate vegetation maps. Indeed, the Waterberg is diverse and vegetation structure and composition changes considerably across the region. For example, the vegetation grouping seen in LWNR differs from Marakele National Park in both vegetation structure and species composition. Therefore, this heterogeneity in the vegetation of the Waterberg may explain why the vegetation-environment relationships documented in LWNR could not be accurately extrapolated to surrounding areas. However, while the mapping ruleset for LWNR may not be effective at mapping vegetation in the surrounding areas, the sampling and analytical techniques used here could easily be replicated across broader areas to repeat this classification and mapping process for larger areas within this region.

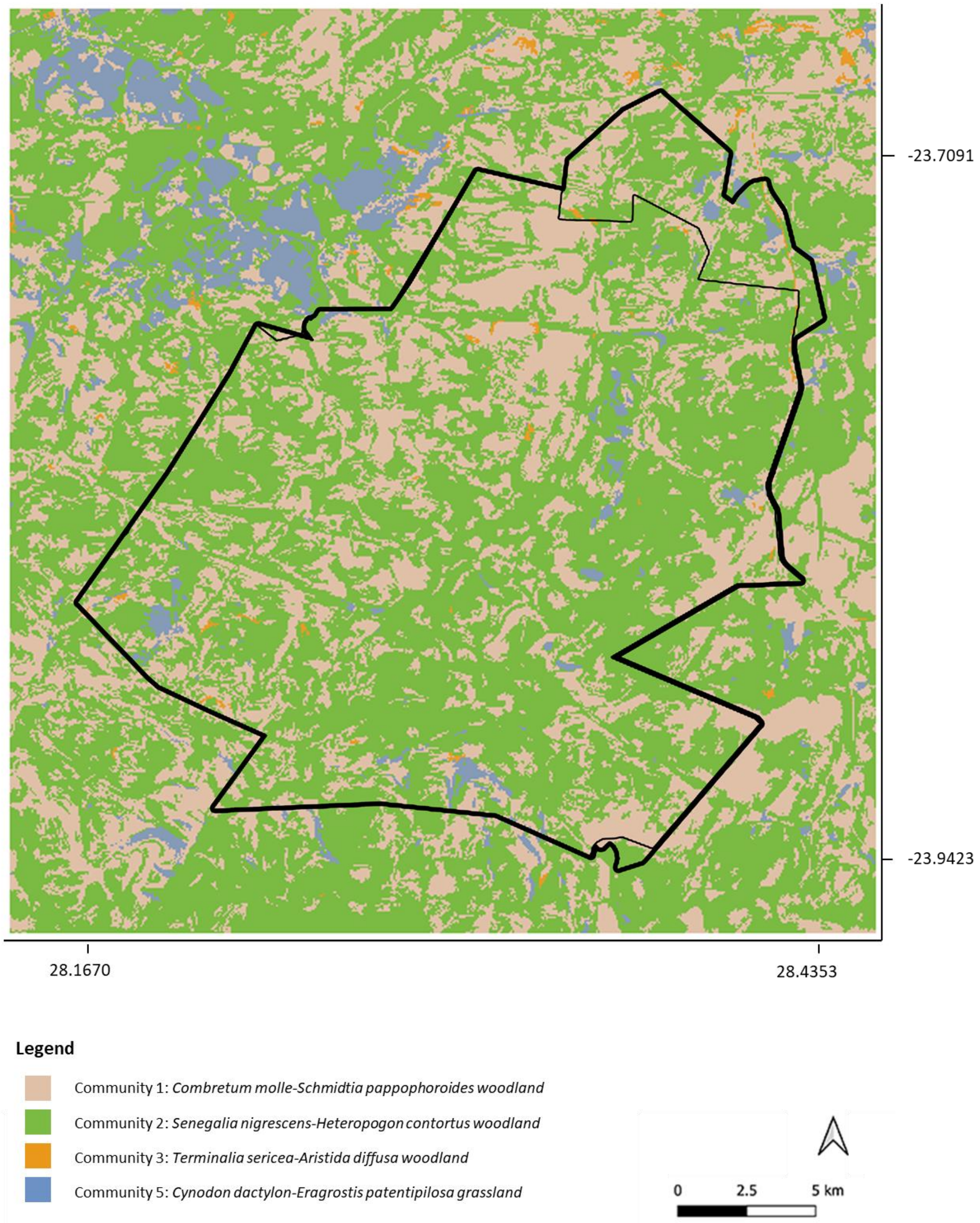

Figure 26. Vegetation map of the area surrounding LWNR, including additional land acquired by LWNR since the original map was created. The thick line indicates the current border of LWNR, with recently acquired land (north-eastern sector) separated from the original extent of the reserve by the thinner border line.

Long term monitoring of vegetation, and periodically updating classifications, is essential for management of vegetation. Vegetation is dynamic, with plant assemblages responding to changes in climate (temperature, moisture), atmospheric CO_2 concentrations, nutrient availability and disturbances (Peng, 2000; Feng and Chai, 2008). Understanding how vegetation is changing over time (i.e. shifts in community composition and structure) is necessary to adjust management protocols (Benedetti et al., 1994; Feng and Chai, 2008). Year-to-year variation in plant communities may be driven by, for example, interannual variation in rainfall and herbivory (Gibson, 1987). Repeated sampling within and across years would account for year-to-year differences in vegetation and give a more complete estimate of species richness and composition, and greater insight into how vegetation in a study area responds to climatic factors (Gibson, 1987; Cao et al., 2014). However, re-analysing my LWNR data using data from tree and grass species only, which have lower year-to-year variability than the more species-rich forbs, resulted in a similar classification. As a result, more intensive sampling of the existing relevés (e.g. repeated sampling of species composition in years of wetter or drier than average conditions) is not expected to change the classification reported here. In contrast, the recent re-introduction of elephants into LWNR may warrant re-sampling of this study’s relevés in the near future since these mixed feeders selectively knock down tree species and, as a result, may change vegetation composition and structure rapidly (Valeix, 2011; Watson, 2020). Indeed, the removal of species favoured by elephants (especially diagnostic or prominent species such as *Senegalia nigrescens;* Watson, 2020) could change the distribution of the vegetation communities over relatively short time scales. The data is available to LWNR to be used as a baseline for future studies such as these in the reserve.

Further sampling and analyses based on additional data could be used to extend and refine this classification (Wiser and De Cáceres, 2013). The classification completed in this study represents the broad vegetation patterns of LWNR, but this can potentially be refined with the addition of other types of data. The classification in this study was based on species composition and a coarse measure of canopy structure. However, in this system there were not many species exhibiting high fidelity (i.e. species composition overlapped largely between communities) and the canopy height classes measured were inadequate to reflect differences in tree height between communities (e.g. the “>4 m height” canopy layer category was inadequate to distinguish the taller *Senegalia nigrescens-Heteropogon contortus* woodland from the dominant *Combretum molle-Schmidtia pappophoroides* woodland). Adding more criteria to the classification, such as physiognomy (including growth forms, leaf characteristics, and/or phenology; Dansereau, 1957; Beard, 1978), or plant functional traits (e.g. specific leaf area, rooting type, photosynthetic pathway, wood density; Bailey and Sinnott, 1916; Gillison, 2002; Traiser et al., 2005; Yang et al., 2015), could give greater insight into a) how vegetation changes spatially, b) what is driving these changes, and c) the adaptive response of vegetation (Suding and Goldstein, 2008; Giorgis et al., 2017). For example, observations in the field show that broader-leaved woody species seemed to be associated with Community 1, and finer-leaved woody more associated with Community 2 (suggesting, for example, differences in nutrient availability between these two communities; Wigley et al., 2018). Additionally, the specific leaf area and leaf matter dry content of grass species within LWNR has demonstrated community-level variation, which is driven by environmental factors including soil pH and potassium (De Beer et al., under review).

I would also recommend targeted supplementary floristic sampling to improve the classification. A consequence of the random sampling design (even when stratification is used) is that localized and scarce plant communities are typically poorly sampled (or not even sampled at all; Wiser and De Cáceres, 2013). This is seen in this study with Communities 1 and 2 being very well sampled (making up 77 % of sampled relevés collectively), but Communities 5-10 poorly sampled (making up only 7 % of sampled relevés collectively). Moreover, poorly sampled communities may have too few relevés for statistical analyses (such as the identification of diagnostic species, environmental drivers etc.) to be accurate (Pignatti, 1980; Roleček et al., 2007; Wiser and De Cáceres, 2013). Some of the poorly sampled communities were observed at other sites within LWNR (for example, Community 9 was only sampled once but was observed in at least three different locations within the study area) and sampling these areas would be useful to more accurately identify diagnostic and prominent species for these communities. This targeted (i.e. preferential) sampling of Communities 5-10 would also enable a more accurate test of which environmental conditions are associated with these communities and could be expected to increase the overall accuracy of the classification.

Future vegetation classification projects in this region should consider using additional environmental variables to stratify sampling areas prior to randomizing the locations of relevés. In this study I used elevation, aspect, slope and soil type to stratify the area, but given the findings of this research, it could potentially be more effective to stratify by additional variables as well. For example, soil characteristics (an important driver of vegetation in LWNR) are often correlated with terrain attributes such as contributing area, stream power index, slope gradient and compound topographic index (see Gobin et al., 2001). Equally, observations in the field showed that the canopy height and structure differed between communities and Lidar data could be used to stratify the sampling area by these vegetation properties too (Hawbaker et al., 2009). A visual inspection of remotely sensed imagery was not useful for identifying unique areas of vegetation prior to sampling at LWNR, but for other areas in the Waterberg with more structurally heterogenous vegetation (e.g. with forest, grassland or wetland habitats) the *a priori* placement of relevés to sample these localized communities based on remotely sensed imagery could be a pragmatic and efficient supplementary sampling strategy.

As a whole, the distribution of the vegetation types of LWNR cannot be well explained by the environmental variables measured in this study. Disturbances, both anthropogenic and natural (e.g. fire and herbivory), are important drivers of vegetation dynamics in some systems (Remmel and Perera, 2001; Wisdom et al., 2006; Grondin et al., 2014), and may contribute to the vegetation patterns currently observed in LWNR, especially since the reserve has gradually incorporated new lands since its initial creation. As a result, different parts of the reserve have varied past land uses (including crop farming, hunting reserves and game farming) and differ in the duration since the land use was switched to solely being conservation- and game-breeding focused. Accounting for the previous land use of each sector of the reserve and the anthropogenic disturbances that occurred (using old maps, surrounding farmers' knowledge and historical aerial photographs, etc.), may give additional insight into the vegetation patterns observed in this study. For example, the distribution of Community 5 appears to be linked to previous agricultural activities (specifically to ploughed fields) and other human influences. Equally, some of the unique communities may have been created or strongly driven by anthropogenic influences (e.g. farming activities or old homesteads) and disturbances (e.g. areas with frequent fires). Contrary to expectations (e.g. Hoffmann et al., 2012), fire history (i.e. frequency and time since last fire) did not contribute to explaining the occurrence of the vegetation types across LWNR. Using Advanced Very High Resolution Radiometer and Normalised Difference Vegetation Index (AVHRR/NDVI) methods has proven to be a more effective method for detecting fires (as compared to MODIS which was used in this study; Remmel and Perera, 2001) and may show fire to have a stronger explanatory power than previous found. Equally, adding data on seasonality and/or intensity of fires may also help to better explain vegetation variation in this system (McLauchlan et al., 2020)

Only four vegetation units were mapped, but future studies could aim to increase the number of units mapped in order to more accurately direct land use planning. Coarse spatial resolution satellite imagery has proven inadequate in some circumstances to accurately predict vegetation (see e.g. Harvey and Hill, 2001). However, in some habitats, increasing the resolution of remotely sensed data does not improve the accuracy of vegetation maps (Marceau et al., 1990; Gong and Howarth, 1992). As the influence of the resolution of satellite imagery has not been assessed in this study, it may be worthwhile formally testing if finer-scale data could lead to a map which includes the smaller patches of unique vegetation communities. Equally, adding more products to the mapping process, such as Lidar, UAV-obtained aerial imagery and NDVI, could also potentially increase the mapping accuracy (Wang and Tenhunen, 2004; Ussyshkin and Theriault, 2011; Su et al., 2016).

There is considerable potential for future herbivory- and biodiversity-focused research to build on this vegetation classification. Vegetation composition and the grazing quality of the species within each community may strongly affect habitat selection (and carrying capacity) of large mammalian herbivores (Miller and Buss, 2015). This research can guide management protocols for specific animals in an area (such as the white and black rhinoceros which require different habitats; Pienaar, 1994; Miller and Buss, 2015) and aid researchers by, for example, guiding where to place camera traps (Cody, 1981; Watson, 2000; Reid et al., 2007; Burkepile, 2013). Equally, as vegetation creates habitat for fauna, it could be expected that composition of some taxa may follow similar distributions patterns to the observed distribution of vegetation. As a result, investigating the biodiversity of the rare communities and isolated patches of vegetation may uncover unique communities of invertebrates and other species with limited dispersal potential.

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