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Lichen morphospecies diversity and community composition across the Tswalu Kalahari Reserve, South Africa

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ABSTRACT

The Tswalu Kalahari Reserve in the Northern Cape Province of South Africa has no previously published data on its lichen biota, which reflects the broader status of lichenology in South Africa. It is estimated that nearly half of the country's lichen species remain undescribed. Consequently, this study aimed to gather baseline data on lichen diversity and distribution across the reserve. We quantified morphological and functional diversity, characterized lichen communities, and analyzed relationships between lichen diversity and environmental variables (northness, coverage, elevation, insolation, site, substrate type, and substrate texture) using morphospecies concepts. We documented 49 morphospecies across three habitats in the Tswalu Kalahari Reserve, including at least one species that is new to science (*Caloplaca tswaluensis* Fryday, S. Svoboda & D. A. Ward; Fryday et al. in press) and another (*Trapeliopsis glaucolepidea* (Nyl.) Gotth. Schneid.) that had not previously been reported from Africa. Overall, we recorded lower diversity in corticolous (bark dwelling) lichen communities compared to saxicolous (rock dwelling) lichen communities. However, we did not find a significant effect of any measured environmental variable on saxicolous species richness. This preliminary study underscores the need for further investigation of the diverse, unrecorded lichen diversity that likely exists in other areas of the country as well as the differences in lichen communities on bark and rock substrates. This study also shows that morphospecies concepts can be informative and accessible approaches for exploratory lichen studies, particularly in regions with relatively understudied cryptogam communities.

1. Introduction

Lichens are common components of terrestrial environments, and can have a range of impacts on ecosystem processes (Asplund and Wardle, 2017). In arid and semi-arid environments, lichens contribute to rock weathering (Guglielmin et al., 2011; Lopez and Bacilio, 2020), nutrient cycling and availability (Evans and Ehleringer, 1993; Rogers et al., 1966; Root et al., 2021; Tian et al., 2023), and soil stabilization (Lopez and Bacilio, 2020; Rodriguez-Caballero et al., 2022). Lichens in these environments exhibit a diversity of forms related to their functions, ranging from thin soil crusts to foliose epiphytes. Variations in functional traits correspond to differences in ecological impacts. For example, the colours of saxicolous lichen thalli have been shown to variably affect rock surface temperature and weathering (Carter and Viles, 2004).

Despite their ecological importance, lichens are often poorly studied in comparison to sympatric plant and animal biotas. Not only are their impacts frequently underestimated and, therefore, less studied, but lichens are also notoriously difficult subjects to identify. These challenges are evidenced by the incomplete checklist of lichens reported from South Africa (Ahti et al., 2016; Fryday, 2015). The current version contains 1751 species but is thought to represent only about half of the species occurring in the country (Ahti et al., 2016; Crous et al., 2006; Fryday, 2015). The checklist relies heavily on literature reports – often from more than a century ago – and consequently, lichenologists have called for the need to verify species occurrences in the field because taxonomic concepts have changed considerably over the intervening years. Recent field surveys combined with molecular work continue to add new species, and even

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genera, to the checklist, pointing to the importance of increased attention towards lichen surveys in southern Africa (Fryday et al., 2020; Medeiros and Lutzoni, 2022).

Although recent attention has resulted in taxonomic advances, the still incomplete understanding of the region's lichen biota contributes to deficits in other research areas, including lichen ecology. Lichen ecology studies in southern Africa have been sparse, with only 12 studies appearing in a search for "ecology" and "South Africa" on the *Recent Literature on Lichens* database (https://nhm2.uio.no/botanisk/lav/RLL/RLL.HTM), which aims to include all scientific literature on lichens since 1536.

Ecological studies that do exist have provided valuable information regarding lichen survival and interactions with their environments. Lichens are known to have several mechanisms for tolerating low precipitation and the resulting desiccation in arid and semi-arid environments, including dormancy, rapid recovery, and biochemical protections such as powerful antioxidant systems and specific proteins (late embryogenesis abundant proteins (LEAs); Gasulla et al., 2021). Although some lichen species can survive environmental extremes, not all lichens exhibit this hardiness. Thus, individual species' spatial distributions can be uniquely shaped by various interacting environmental factors including humidity, insolation, elevation, light, and air quality (Zedda and Rambold, 2009; Zedda and Rambold, 2015; Zedda et al., 2011).

Lichens with unresolved taxonomy or those that require significant resources and expertise to identify can be challenging study subjects. However, in the absence of taxonomically precise information, lichen morphospecies – that is, classifying a lichen by its macromorphological characters – can provide useful units of classification, particularly for exploratory studies. In the face of rapid biodiversity loss and increasing community science engagement through platforms such as iNaturalist (www.inaturalist.org), documenting biodiversity without reliance on taxonomic expertise or resources is a relevant need.

The present study is an exploratory project in response to the Tswalu Kalahari Research and Conservation team's interest in the diversity of its locally occurring lichens. The primary aim was to describe the lichen diversity and provide preliminary insight into the lichen communities of the reserve. We sought to address three main questions: (1) what is the quantifiable diversity of lichens at the Tswalu Kalahari Reserve? (2) what lichen communities are present? and (3) what is the relationship between selected environmental variables and lichen diversity?

2. Materials and method

2.1. Study area

Tswalu Kalahari Reserve is a 1020 km^2 conservation area in the Northern Cape province of South Africa and is located within the southern Kalahari Desert (27.2031°S, 22.4673°E). This region falls within the semi-arid savanna biome and is characterized by its relatively low annual rainfall of around 300 mm, which varies according to the season and location within the reserve (Tswalu Kalahari Reserve Rainfall database). Annual rainfall ranged from about 160 to 615 mm per year between 1998 and 2006 at the Tswalu Kalahari Reserve's Gosberg rain gauge (27.2660 °S, 22.4458 °E), which is close to the center of the localities we sampled in this study (Fig. 1; Tswalu Kalahari Reserve, 2024). The Kalahari Desert experiences a seasonal environment with most rainfall occurring during the summer from November to March (Fig. 1). The spatial distribution of precipitation shapes vegetation patterns across the reserve, ranging from dune grasses to thickets, which are broadly classified as part of the Eastern Kalahari Bushveld Bioregion (Mucina et al., 2018; Schoville et al., 2023).

Tswalu Kalahari Reserve's unique geology also shapes patterns of natural communities across the landscape with several distinct formations characterizing the geology of the reserve. While the majority of the ground surface at the Tswalu Kalahari Reserve is covered by wind-blown sand, there are three major geologic features associated with the Matsap formation in the Groep Volop Group (Moen, 1977). Alternating layers of quartzite and subgraywacke sandstone bisect the reserve from north to south (Moen, 1977). Coarse-grained quartzite, subgraywacke, and conglomerate extend eastward and a relatively small section of coarse-grained subgraywacke and conglomerate exists to the west of the bisecting quartzite and subgraywacke (Moen, 1977). Dolomite/sandstone outcrops are generally found on the eastern side of the reserve and are less common than the sandstone/quartzite formations (Schoville, 2023). The altitude across the reserve ranges from 1586 m on Korannaberg Mountain to 1020 m in the plains habitat (Davis et al., 2010).

We restricted this study to four sites in three distinct habitat types at the Tswalu Kalahari Reserve (Fig. 2). These sites were thought to represent the reserve's lichen diversity according to observations by reserve staff members. Three of the four sites represented saxicolous lichen communities, one represented a corticolous community and none represented terricolous communities given we found very few soil dwelling lichens on the large swaths of loose sands across the reserve (Fig. 2). Sites 1 and 2 occur at the sandstone/quartzite hills at North Gosberg and Verwater. Sandstone/quartzite outcrops are found scattered throughout the reserve and are colonized by saxicolous lichens and occasionally liverworts at the bases of rocks. Site 3 occurs within the Olifantshoek Plains Thornveld vegetation at District Road. Olifantshoek Plains Thornveld is characterized by scattered trees and shrubs with a grass dominated ground layer and is the dominant vegetation type of the Kalahari (SVk 13; Mucina et al., 2018). Site 3 is suspected to be the location of the highest corticolous lichen diversity in the reserve according to Tswalu Kalahari Reserve staff observations and it represents the only corticolous community in the study. Site 4 falls within dolomite/sandstone rock outcrops at the Legkaba section of the reserve (Fig. 3). The average elevation of the sites is 1231 m and it ranges from 1135 m at Site 4 to 1293 m at Site 2.

2.2. Sampling

We chose a sampling methodology with the goal of rapidly and quantitatively assess lichen morphospecies diversity at each site within the reserve. For the rock sampling (Sites 1, 2, and 4), we randomly tossed 0.25 × 0.25 m quadrats onto rocks, irrespective of their aspect or slope, to capture the saxicolous lichen communities' profiles. For the bark sampling (Site 3), we placed 0.25 × 0.25 m quadrats 1.5 m from the ground on the south-facing aspect of the tree trunk. At both rock and bark sites, we counted the number of morphospecies within each quadrat and estimated the percent of the quadrat covered by lichens. At each quadrat, we recorded elevation, aspect, insolation (amount of sunlight), substrate texture, tree circumference, and substrate type (tree or rock). We calculated northness using the cosine of the aspect so that every northness value ranged from −1 and 1 for ease of interpretation. We measured insolation and substrate texture ordinally on scales of 1 to 6 and 1 to 3, respectively. We documented reproductive structures of each morphospecies as vegetative, sexual, or none seen. We assigned photobiont identity using the general taxonomic identity of each lichen based on basic knowledge by the field team and recorded it as either green algal or cyanobacterial. We collected and vouchered lichens that could not easily be determined in the field or lichens that were of interest to the field team and deposited the vouchers in the herbarium of North-West University (Mahikeng), South Africa (UNWH).

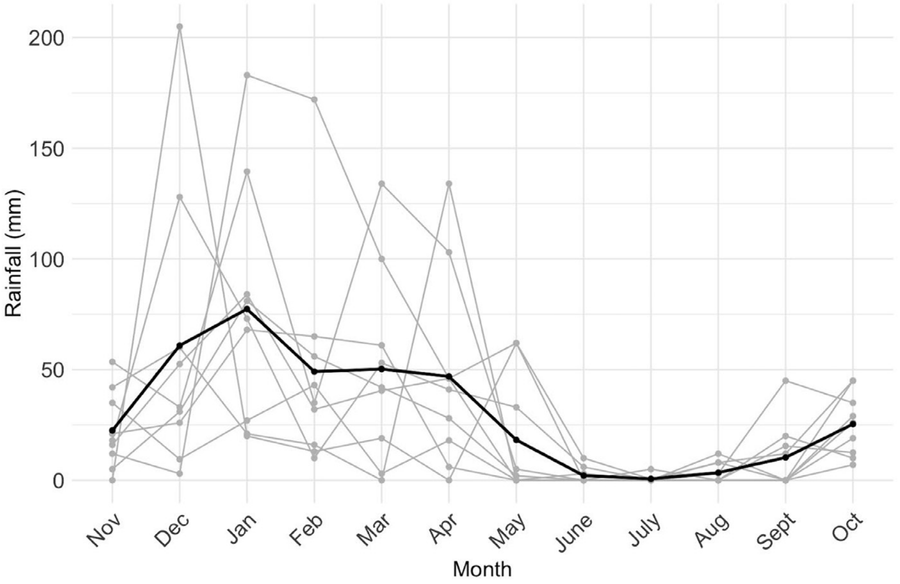

Fig. 1. Monthly rainfall (mm) at the Gosberg rain gauge, Tswalu Kalahari Reserve (27.2660 °S, 22.4458 °E) from 1998 – 2006. Grey lines represent rainfall in a given year and black line represents average across all years.

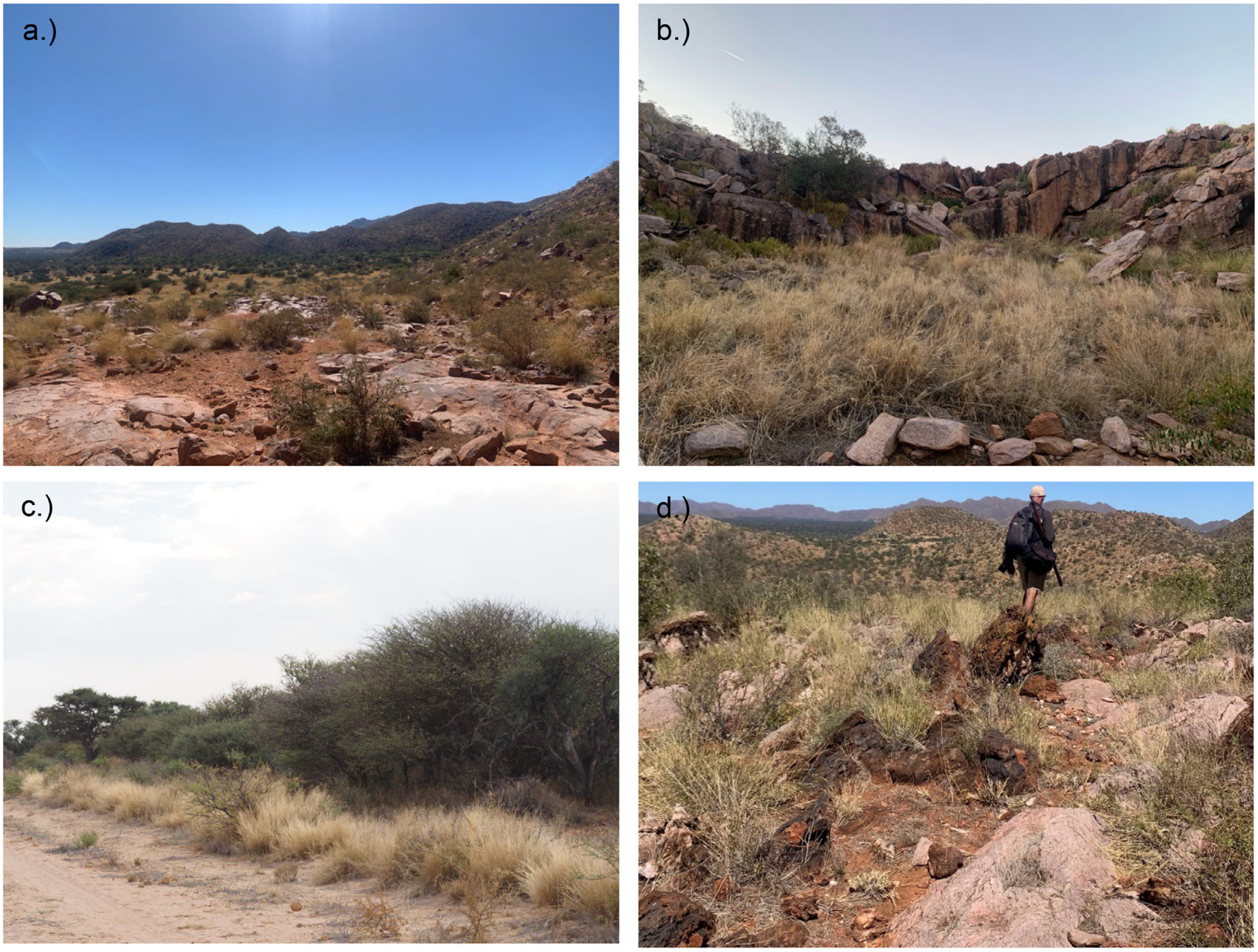

Fig. 2. Habitats of each of the four sampling sites within the Tswalu Kalahari Reserve a. Site 1 “North Gosberg”; b. Site 2 “Verwater”; c. Site 3 “District Road”; d. Site 4 “Legkaba.”

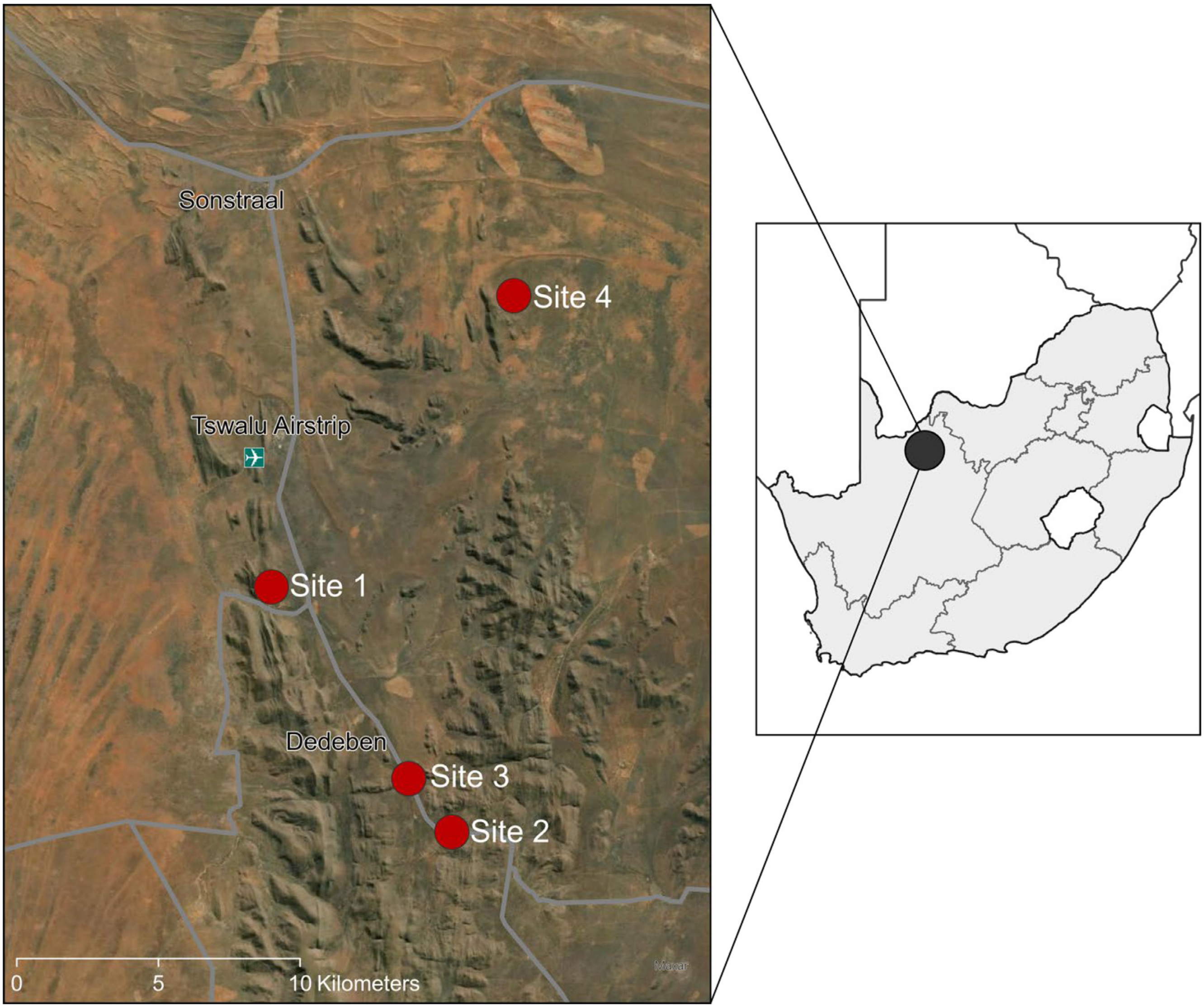

Fig. 3. Four sampling sites (red circles) in the Tswalu Kalahari Reserve in the Northern Cape Province of South Africa.

2.3. Data analysis

To investigate patterns of diversity at local and landscape scales, we quantified three levels of diversity (alpha, beta, and gamma) based on morphospecies presence/absence data from our field sampling. We calculated alpha diversity as the number of morphospecies in each quadrat. We calculated beta diversity at each site as species turnover between quadrats using Whittaker's Index with the betadiver function in the vegan package in R (Whittaker, 1960; Oksanen et al., 2022; Fig. S1). Whittaker's Index is the proportion by which the species richness of an area exceeds the average richness of a single locality within that area and is calculated as:

$$\frac{(b+c)}{(2a+b+c)}$$

where a represents the number of species that are common to both communities, b represents the number of species unique to the first community, but not present in the second community, and c represents the number of species unique to the second community, but not present in the first community. Whittaker's beta diversity ranges from 0 to 1.0, which corresponds with none to complete variation between quadrats, respectively. We calculated gamma diversity as the total number of morphospecies observed at each site.

We restricted the community and environmental analyses to the three saxicolous lichen sites (Sites 1, 2, and 4). We excluded the corticolous lichen site (Site 3) because saxicolous and corticolous lichens may be impacted differently by environmental variables and including them in one analysis may misattribute any impacts. We assessed community composition of saxicolous lichens using non-metric multidimensional scaling (NMDS) ordinations based on Jaccard distances of morphospecies presence/absence data at each quadrat. We overlaid environmental vectors on the sampling points to investigate the relationship between lichen communities and environmental variables.

We used a causal inference framework to infer which environmental variables affect lichen morphospecies richness and how these interactions might be confounded by other variables (Arif and MacNeil, 2022). We identified a number of measured (elevation, northness, insolation, coverage, substrate type, slope, and substrate texture) and unmeasured (precipitation, soil type, and exposure to trampling) environmental variables as potential drivers of lichen richness. We modelled the relationship between each measured environmental variable and quadrat morphospecies richness using generalized linear models (GLMs) with Poisson distributions and a fixed effect for "site". We included potential confounding variables as fixed effects in the models. In total, we ran four models assessing the effects of environmental variables on lichen richness. We also examined the relationship between morphospecies richness and percent coverage of the quadrat by lichens. We calculated p-values for fixed effects using likelihood ratio tests, defining significance where $p < .05$. All analyses were done in R (version 4.3.2, R Core Team, 2023) using the vegan and ggplot2 packages (Oksanen et al., 2022; Wickham, 2016).

3. Results

In total, we recorded 49 morphospecies across the four localities - 42 at the saxicolous sites and 7 at the corticolous site. We recorded high spatial turnover with 78 % (n = 38) of all recorded morphospecies occurring at a single site, 16 % (n = 7) at any two sites and 6 % (n = 4) at any three sites. No morphospecies occurred in all four sites. Among all observed lichens, a black crustose morphospecies was the most common (found in 33 % of all quadrats, n = 13), and a morphospecies of *Acarospora* A. Massal. was the second most common (found in 28 % of all quadrats, n = 11, Fig. 4). We did not record any morphospecies that occurred in both the corticolous and saxicolous communities. Across all sites, crustose was the most common growth form (53 %, n = 26), followed by foliose (35 %, n = 17), and squamulose (12 %, n = 6). We only recorded 1 crustose and 1 squamulose morphospecies in the corticolous site (Site 3) with the majority being foliose (n = 5). Foliose and squamulose growth forms were rare in the saxicolous communities (29 %, n = 12 and 12 %, n = 5, respectively), which were otherwise dominated by crustose lichens (60 %, n = 25). Across all sites, 94 % of surveyed lichen had green algae photobionts (n = 46), whereas the remainder had cyanobacteria (n = 3). Most lichens had sexual reproductive structures (80 %, n = 39), versus 20 % (n = 10) with vegetative reproductive structures. However, this result varied at the site level where we recorded that 86 % (n = 36) of the lichens in the saxicolous sites had sexual reproductive structures, and 43 % (n = 3) of the lichens in the corticolous site had sexual reproductive structures. The average percent cover by lichens in the quadrats was 64 % across all the sites with 65 % in the saxicolous sites and 54 % in the corticolous site. Cover ranged widely from 20 % to 95 % in the saxicolous sites and 5 % to 80 % in the corticolous site.

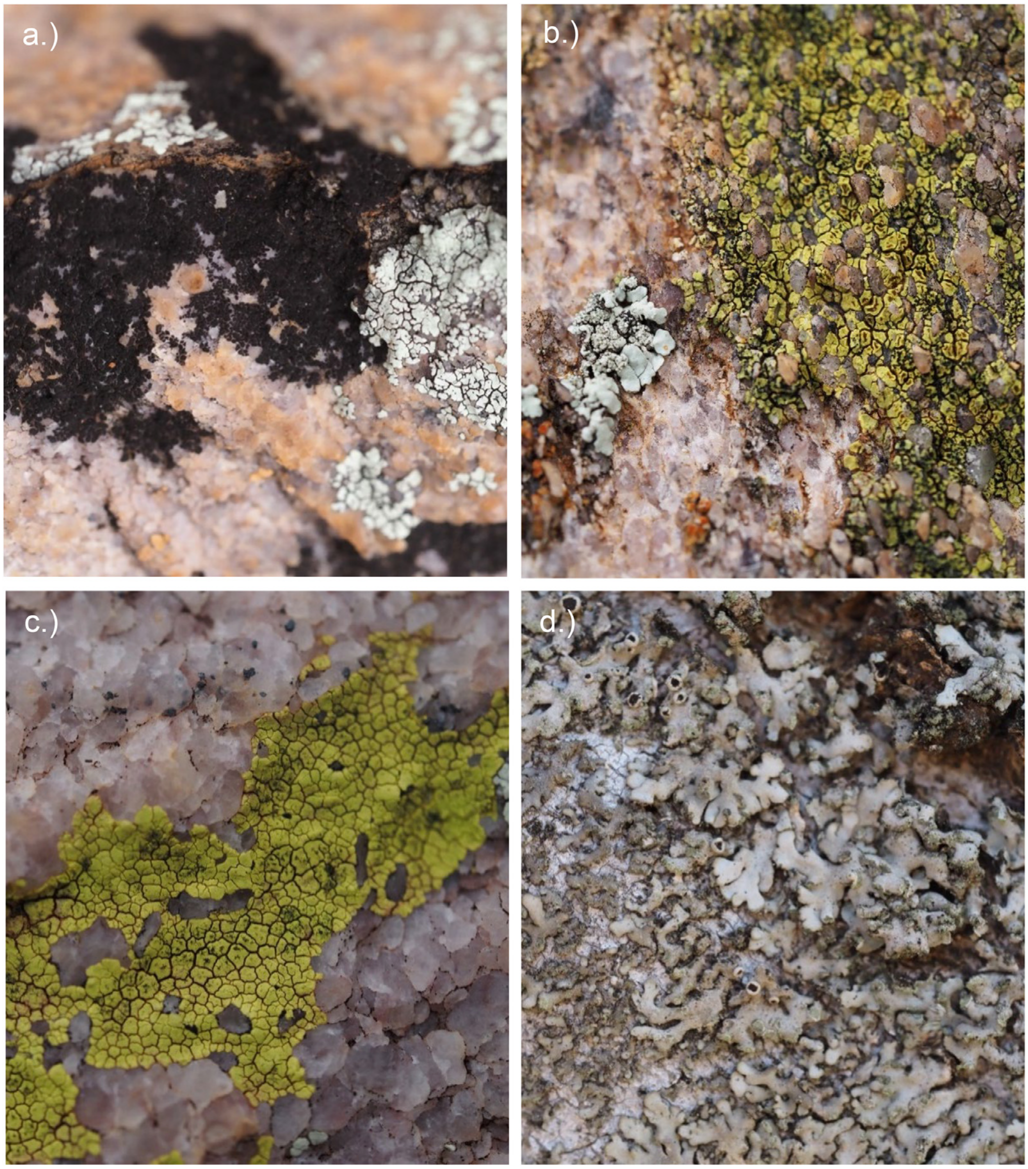

Fig. 4. The four most commonly occurring lichen morphospecies (MS) across the four sites. a. “Black MS 1” occurred in 13 of 40 quadrats; b.“*Acarospora* MS 1” occurred in 11 of 40 quadrats; c. “*Acarospora* MS 2” occurred in 9 of 40 quadrats; d. “*Phaeophyscia orbicularis* 1” occurred in 8 of 40 quadrats.

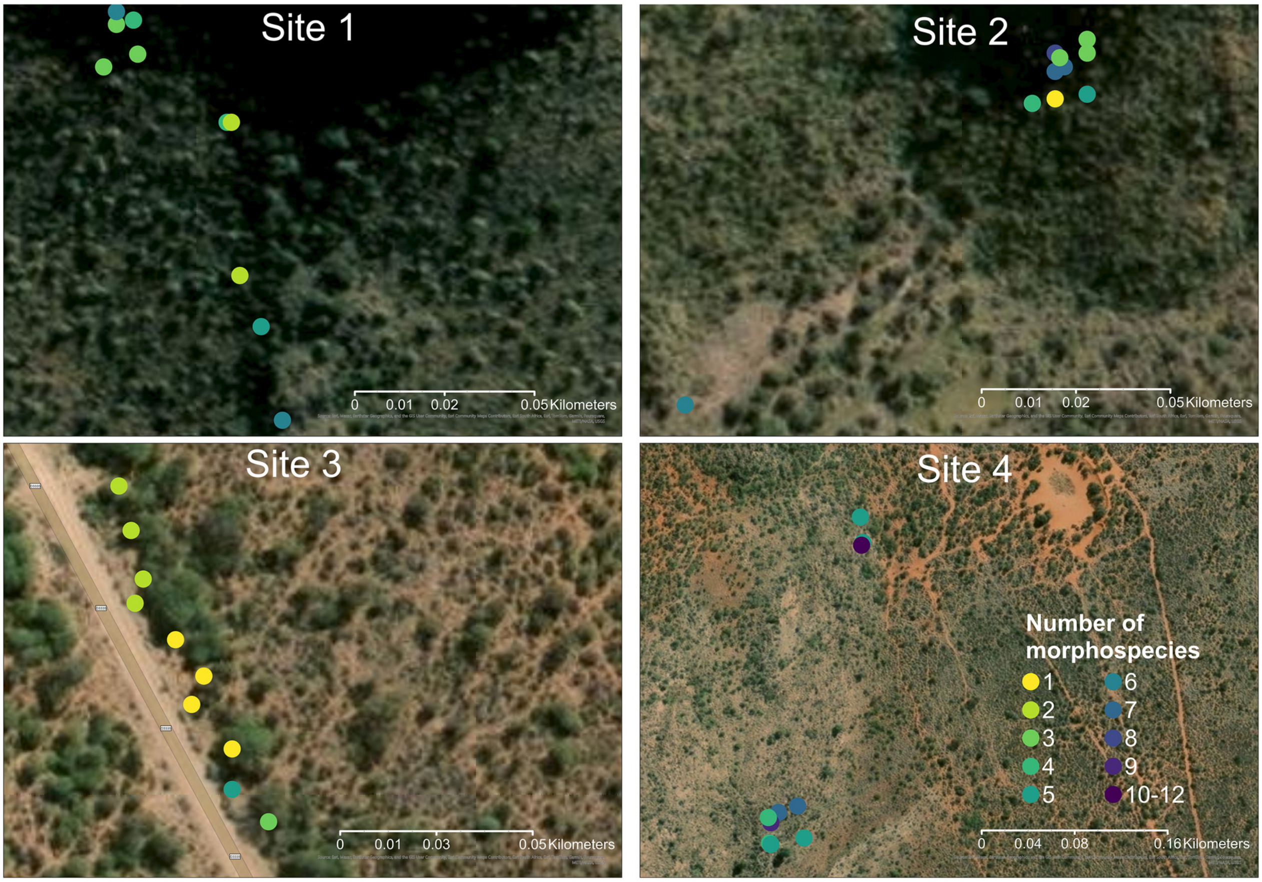

Fig. 5. Alpha diversity on quadrats at four sites in the study area. Coloured circles correspond to alpha diversity (number of morphospecies per quadrat).

3.1. Morphospecies diversity

Alpha diversity ranged from an average of 2.0 morphospecies per quadrat at Site 3 to 6.0 morphospecies per quadrat at Site 4 (Fig. 5; Table 1). Average beta diversity between quadrats ranged from 0.14 to 0.35 across the four sites. Like alpha diversity, the lowest average beta diversity was recorded at Site 3 and the highest at Site 4 (Table 1; Fig. S3). Gamma diversity ranged between 7.0 at Site 3 and 20.0 at Site 1 (Table 1). Sites 1, 2, and 4 all shared similar alpha and gamma diversity values in comparison to Site 3.

3.2. Community composition of saxicolous lichens

The NMDS plot shows some overlap among the quadrats with the strongest overlap among points from Sites 1 and 2 and some overlap with points from Site 4. Sites 1 and 2 were located in sandstone/quartzite outcrops and the substrates were qualitatively the most similar at these two sites. The difference between Site 4 and the other sites is associated with the substrate texture vector, suggesting that substrate microtopography might have impacted lichen community composition among the saxicolous lichens (Fig. 6). Specifically, the texture of the dolomite rock at Site 4 was rougher than the sandstone at Sites 1 and 2. Northness was the only variable that was not included by the ordination, suggesting it is not a strong driver of lichen community composition at the sites. While there is not a strong separation of sites when sampling only saxicolous lichens, there is a clear distinction between the saxicolous and corticolous lichen sites when all four sites are included in an NMDS plot (Fig. S2).

3.3. Influence of environmental variables on saxicolous lichen diversity

We did not find any identifiable relationship between the examined environmental variables and saxicolous morphospecies richness (Fig. 7). However, we recorded significantly higher richness at Site 4 compared to the other sites (Table S3). This richness may be driven by an unmeasured environmental variable as it was not explained by any of the measured variables included in our models.

Table 1
Diversity of lichen morphospecies at four sites within the Tswalu Kalahari Reserve. Alpha, beta and gamma diversity represent the average number of morphospecies per quadrat, the average species turnover between quadrats, and the total number of morphospecies at each site, respectively.

Site	Locality	Substrate	Alpha diversity	Beta diversity	Gamma diversity
1	North Gosberg	Rock (sandstone/quartzite)	4.0	0.31	20.0
2	Verwater	Rock (sandstone/quartzite)	5.0	0.32	18.0
3	District Road	Bark (Olifantshoek Plains Thornveld)	2.0	0.14	7.0
4	Legkaba	Rock (dolomite/sandstone)	6.0	0.35	19.0

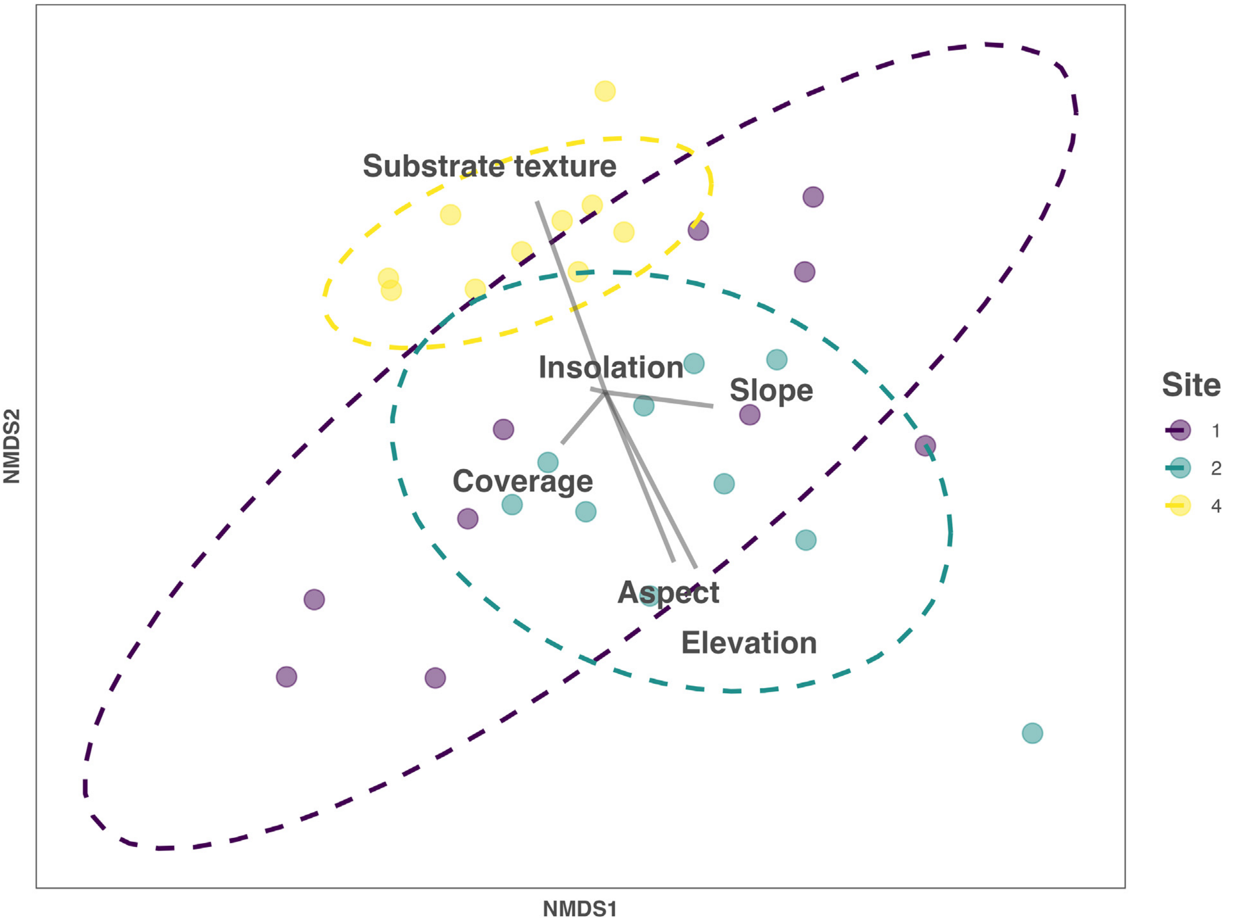

Fig. 6. NMDS plot of saxicolous lichen morphospecies across all four sites with ellipses representing 95 % confidence intervals around the centroid and each point representing a quadrat. Stress value is 0.099.

4. Discussion

Our study addressed a gap in biodiversity knowledge at the Tswalu Kalahari Reserve by documenting the local lichen biota for the first time. The results of our work offer quantitative descriptions of the morphological diversity and functional traits as well as preliminary insight into the environmental variables that drive diversity. While we preliminarily identified lichens using morphospecies concepts, we also identified most lichens to the genus level and 16 lichens to species, including at least one species new to science (*Caloplaca tswaluensis*; Fryday et al., 2024) and another (*Trapeliopsis glaucolepidea*) that had not previously been reported from Africa (Table S1 and Table S2).

We recorded relatively low beta diversities of around 0.3, suggesting similarities between quadrats within each of the four sites. However, we also found that most morphospecies were only found at a single site. These findings suggest that there is similarity within sites and differences among sites, which may be attributable to microhabitats, geographic barriers, or dispersal limitations of the lichens. One way to investigate these potential drivers of differences in community composition is to assess functional traits of lichens.

Our study found that some functional traits were disproportionately represented among lichens sampled at the Tswalu Kalahari Reserve compared to lichens globally. For instance, we recorded crustose lichens in a lower proportion (53 %) than their average representation (67 %) elsewhere (Lendemer et al., 2013; Manzitto-Tripp et al., 2022; Spribille et al., 2020). Non-crustose growth forms are likely overrepresented in our study as a result of our sampling on bark, which supports the highest number of non-crustose lichens in our study. One-quarter of our sites were on bark, but we estimate that bark substrates represent a small fraction of all available lichen substrates across the reserve. An alternative explanation for our potential under sampling of crustose lichens is that they are highly cryptic, and their taxonomic diversity may not have been accurately captured with our morphospecies approach. We rarely sampled cyanobacterial photobionts (2 %); however, cyanolichens represent about 10 % of all lichens globally (Honegger, 2008). This disproportionate representation of traits may relate to a unique functional role of lichens in the Kalahari environment. Cyanolichens fix nitrogen and are more commonly found in humid environments around the globe (Rikkinen, 2015). The Kalahari Desert is semi-arid, and is known for supporting plants and animals that add nitrogen to the environment, such as grazing mammals and nitrogen fixing plants, including *Senegalia mellifera* (Vahl) Seigler & Ebinger in the Olifantshoek Plains Thornveld community. Therefore, cyanolichens may be less likely to fill a functional niche in the dry conditions of the Kalahari Desert. Alternatively, the relative lack of cyanolichens may be associated with inhospitable pH profiles of the substrates. Cyanobacterial photobionts, which are components of cyanolichens, are sensitive to acidic environments (Fritz-Sheridan, 1985; Mulroy et al., 2022). In this study, cyanolichens were more commonly observed on basic dolomite than comparatively acidic sandstone. However, we based our preliminary study on a small sample size, and need further sampling of additional sites to confirm that the reported proportion of functional traits is present at other localities within the Tswalu Kalahari Reserve.

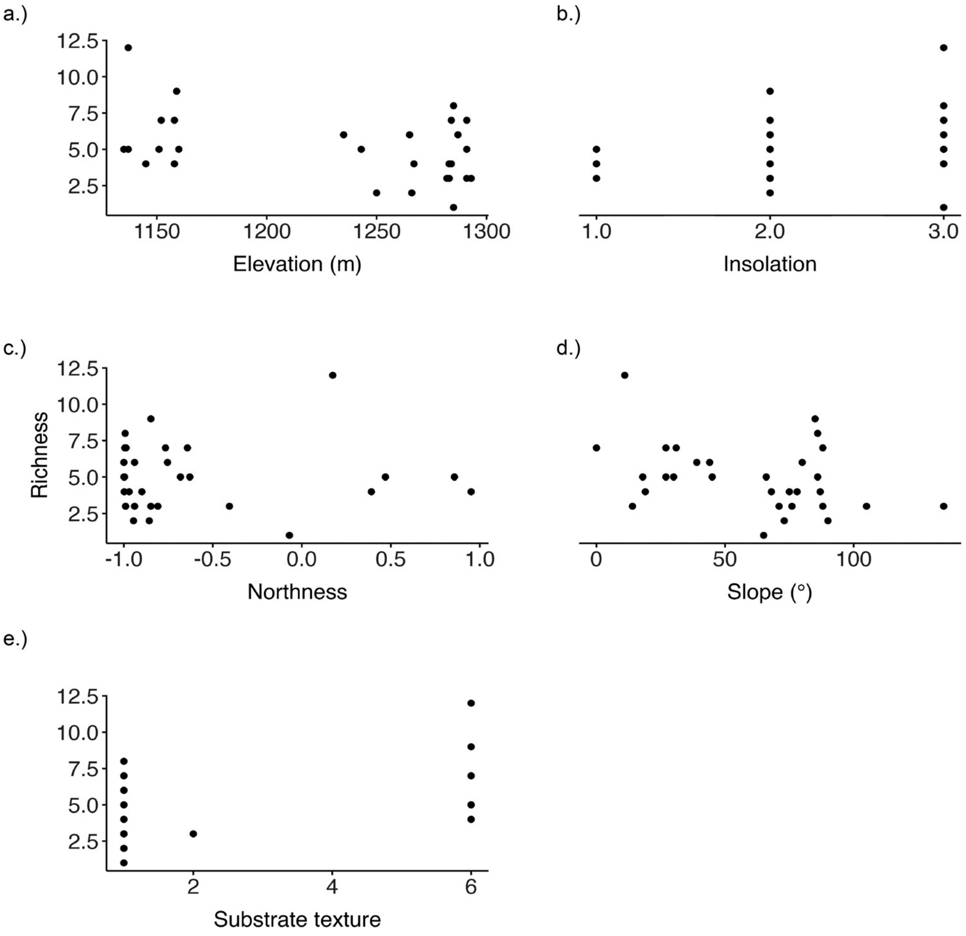

Fig. 7. Relationships between richness (number of lichen morphospecies) on quadrats and quantitative environmental variables: a. elevation (m); b. insolation; c. northness; d. slope (°); e. substrate texture. See methods and Table S1 for model details.

Although sexual reproductive structures were relatively common in our sampling (80 %), this percentage was lower than what is documented for lichens in other regions (90 %) (Purvis et al., 1992). We have difficulty interpreting the high representation of sexual reproductive structures in comparison to vegetative reproductive structures among sampled lichens. Previous studies have reported varied and contradictory relationships between climate and lichen reproductive strategies. Some research has found that lichens produce sexual reproductive structures in hostile environments (Seymour et al., 2005), which supports the findings of this arid environment study. Other work has documented a higher proportion of asexually reproducing lichens in drier environments (Prieto et al., 2017), which is inconsistent with the results of the present study. Notably, the corticolous community site (Site 3) we sampled had a higher percentage of asexual than sexual reproductive structures, while the saxicolous communities all showed higher percentages of sexual reproductive structures. This finding may be related to the potentially more exposed rock substrates that may not be protected enough for lichen propagules to establish. However, many questions surrounded this difference and we believe that further investigation is needed to understand if reproductive strategies are related to environmental conditions in this region.

The lowest alpha diversity was recorded at the single bark site (Site 3) and the highest alpha diversity was recorded at the dolomite rock site (Site 4; Table 1). The dolomite was generally rougher in texture than the sandstone and quartzite surfaces, which may facilitate lichens' ability to adhere to the substrate and increase the number of lichens that could occur on it (Fig. 6; Epstein and Nicholson, 2016). However, we recognize that this relationship may be driven by the higher pH of the dolomite substrate in comparison to the sandstone rather than the substrate texture (Table S1). In addition to pH, elemental composition of a substrate may affect its suitability for some lichens (Brodo, 1973; Mulroy et al., 2022). We sampled corticolous lichens from three tree species (*Vachellia erioloba* (E.Mey.) P.J.H. Hurter, *Senegalia mellifera* (M. Vahl) Seigler & Ebinger, and *Boscia albitrunca* (Burch.) Gilg & Ben). These three species may be characterized by different pHs, and therefore support distinct lichen communities. We recorded the lowest turnover (beta diversity) at the corticolous site (Site 3), which may reflect substrate specificity among corticolous lichens in comparison to saxicolous lichens, which are known to be more generalist (Table 1; Resl et al., 2018). These differences between substrates were also present at the community level, which revealed two main communities of saxicolous and corticolous lichens (Fig. S2). However, we lacked sufficient data to disentangle the impact of substrate and site, or statistically test the effect of substrate on diversity.

While substrate texture was associated with driving the differences across saxicolous lichen communities (Fig. 6), it did not clearly explain the differences in saxicolous morphospecies richness at each site (Fig. 7). None of the measured variables explained the differences in morphospecies richness, and our study may not have captured environmental conditions that influence lichen richness. For example, precipitation was identified as a potential confounding variable for substrate and substrate texture, which suggests that precipitation is an important variable to measure in further investigations (Table S1). Similarly, lichens are known to be sensitive to air quality, and we did not measure any indices of air quality. Future studies would benefit from including these environmental variables to understand what drives lichen assemblages and how they can be used in monitoring, particularly in arid regions in the face of climate change (Ndlovu et al., 2019).

A limitation of our diversity analyses is that alpha, beta, and gamma diversity may be ineffective for comparison across studies and regions beyond an individual study if sampling scales are not congruent (McCoy and Heck, 1987). Similarly, these measurements may capture the effects of small-scale community dynamics such as competitive exclusion and spatial clustering, which may not serve as representative of the overall diversity in the environment (Vellend, 2001).

In this study, we showed that morphospecies concepts can be a valuable and accessible approach to characterizing an area's lichen biota. Our morphospecies approach used an easily repeatable protocol that does not require taxonomic expertise or significant resources. Our findings corroborate other studies that have found that morphospecies and functional traits are reliable concepts for assessing and quantifying lichen diversity (Giordani and Brunialti, 2015; Giordani et al., 2009; Zedda et al., 2011; Pérez-Carrascal et al., 2019). While morphospecies concepts can be useful, low barrier approaches to addressing baseline diversity questions, morphological diversity and phenotypic plasticity within a species may complicate the reliability of these methods (Giordani et al., 2009). As a result, morphospecies concepts are inappropriate in addressing questions that depend on precise taxonomy. Many studies that utilize taxonomic precision address important questions and we see exploratory morphospecies studies as complements to taxonomic approaches.

5. Conclusion

The first study of the lichen diversity at the Tswalu Kalahari Reserve has presented important preliminary data, including the occurrence of 49 morphospecies across four localities within the reserve. Specific functional traits were disproportionately represented when compared with global patterns, which may be related to the unique function of lichens in the semi-arid savanna biome. We also found that different sites supported distinct lichen communities, with the bark site supporting unique communities and lower diversity compared to the three rock sites, aligning with the knowledge that lichens are generally substrate specific. As a result, we believe the differences between rock and bark substrates play an important role in driving lichen diversity and community composition in the semi-arid Kalahari environment, although this hypothesis could not be statistically tested. We acknowledge that our study presents a preliminary set of results on lichen diversity and community composition as it is derived from limited sampling, and we highlight that this project is hypothesis generating. We recommend that future studies compare the lichen biota across a larger number of sites characterized by different substrates in the region to shed more light on the role of substrate and other environmental variables that influence the lichens of the southern Kalahari. Because our study did not rely on precise taxonomic identifications or require a significant amount of technical equipment or financial support, it can serve as a model for a low-barrier entry point to obtain baseline data for lichens in understudied regions.

Code availability

The code and instructions to perform analyses and generate figures shown in the main text are available at https://github.com/danielleward12/TswaluLichens.

Data availability

The datasets generated and analyzed during the current study are available in the Zenodo database at [https://doi.org/10.5281/zenodo.13887757].

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Danielle A. Ward: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sutapa Adhikari:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Madeleen Struwig:** Methodology, Investigation, Conceptualization. **Sarah Skikne:** Writing – review & editing, Formal analysis. **Alan Fryday:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Dylan Smith:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Nishanta Rajakaruna:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.sajb.2024.10.003.

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