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Heuweltjies as within-paddock indicators of veld condition in the Succulent Karoo: vegetation contrasts between mound and intermound habitats

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ABSTRACT

Heuweltjies (microtopographic earthen mounds) are conspicuous across South Africa's semi-arid, winter-rainfall rangelands, yet their value as field-ready indicators of veld condition is under-tested. This study examines the suitability of heuweltjies as indicators of veld condition within paddocks in the semi-arid Succulent Karoo. We utilized a spatially explicit paired sampling design, comparing vegetation attributes on 16 mounds with adjacent intermound plots (the matrix), in the Ebenhaeser communal rangelands. We focused on operational diagnostics, which are repeatable, management-sensitive metrics derived from life-form balances, growth-form structure, and palatability-weighted abundance. Statistical comparisons utilized Generalized Estimating Equations (GEE) to ensure robust inference by accounting for the non-independence inherent in the paired plot design. Mound habitats consistently showed a strong utilization signal, characterized by significantly higher counts of palatable individuals, as well as high herb richness and Shannon diversity. This confirms the ecological function of heuweltjies as resource islands that concentrate desirable forage. Annual plants exhibited significantly higher abundance and cover on mounds, reflecting their sensitivity to the localized nutrient enrichment and disturbance inherent in these resource islands. Succulent shrubs (a key forage group) were significantly larger on mounds, yet grasses were more abundant on the intermound matrix, highlighting a competitive trade-off possibly driven by higher mound alkalinity or shrub competition. These results validate the inherent mound–intermound contrast as a robust, low-cost indicator framework. Formalizing metrics such as palatable plant count difference and annual proportion provides local managers with repeatable, management-relevant signals necessary for setting accurate utilization thresholds, thus improving the performance of broader veld condition assessments.

1. Introduction

The semi-arid Succulent Karoo Biome of South Africa, a globally recognized biodiversity hotspot characterized by a predominantly winter rainfall regime (Cowling & Hilton-Taylor, 1999; Mucina et al., 2006; Myers et al., 2000), presents significant challenges for rangeland management. Traditional operational assessments rely on equilibrium-based models and static vegetation categories (e.g., decreaser/increaser species (Vorster, 1982)), a framework that proves unreliable in highly dynamic drylands where non-equilibrium dynamics dominated by stochastic rainfall variability prevail (Sullivan & Rohde, 2002; Vesk & Westoby, 2001; Vetter, 2005). Studies confirm that many species exhibit inconsistent grazing responses across sites, such as acting as an increaser in one context and a decreaser in another (Rutherford & Powrie, 2010; Schmiedel et al., 2016; Vesk & Westoby, 2001). Such broad standardized groupings are often considered scientifically unsound and of limited practical utility in specific local contexts, particularly in non-equilibrium rangelands (Sullivan & Rohde, 2002). To improve diagnostic sensitivity, monitoring must pivot toward exploiting spatial heterogeneity by targeting specific *indicator patches* – localized landscape elements that register grazing disturbances more quickly and clearly than the surrounding matrix (Stokes et al., 2009). Site-specific, repeatable diagnostics are essential for complementing regional assessment frameworks (Vesk & Westoby, 2001; Sullivan & Rohde, 2002).

The ecological foundation for using localized indicators rests on the phenomenon of fertility islands, which emerge and persist from coupled

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soil-vegetation feedbacks that are sensitive to disturbance (Schlesinger et al., 1996). This concept is powerfully exemplified globally by termite mounds, recognized as keystone structures and ecosystem engineers that significantly alter soil and resource distribution (Dangerfield et al., 1998; Kunz et al., 2012; McAuliffe, 2023). In African savannas, for instance, mounds formed by Macrotermes species similarly create localized nutrient hotspots (elevated N, P, etc.) (Davies et al., 2024; Grant & Scholes, 2006; Seymour et al., 2014), driving vegetation heterogeneity and concentrating herbivore utilization (Davies et al., 2024).

This functional convergence is mirrored in the semi-arid Succulent Karoo Biome (Rutherford & Powrie, 2010), where large, conspicuous earthen mounds known as heuweltjies (meaning "little hills") occur over extensive areas (Cramer et al., 2012; Kunz et al., 2012). These mounds (heuweltjies), associated with the southern harvester termite, *Microhodotermes viator* (Moore & Picker, 1991; Picker et al., 2007), function as resource islands (Francis & Poch, 2019; Kunz et al., 2012; Midgley & Musil, 1990). They exhibit enriched soil nutrients (carbon, nitrogen, phosphorus) and finer texture compared to the adjacent matrix (Kunz et al., 2012; Midgley & Musil, 1990), creating a unique environment known to be attractive to herbivores and highly responsive to utilization pressure (Armstrong & Siegfried, 1990; Kunz et al., 2012). Heuweltjies' genesis remains debated: Whether they are relict landforms produced by differential erosion (Cramer et al., 2012; McAuliffe et al., 2018) or features formed by vegetation-induced aeolian sediment accretion (Cramer et al., 2016; Cramer & Midgley, 2015; McAuliffe et al., 2014), their remarkable longevity and regular spacing affirm their reliability as persistent features for monitoring (Cramer et al., 2012; Kunz et al., 2012; Moore & Picker, 1991).

The utility of the contrasting heuweltjie mound as an Indicator Patch for resource managers remains underdeveloped in the semi-arid Succulent Karoo. Existing *heuweltjie* studies describing ecological differences (Kunz et al., 2012; Midgley & Musil, 1990) have not consistently translated these into routine monitoring metrics. Furthermore, mound effects are known to be context-dependent across landscapes (e.g., directional and setting-specific expression in savannas (Davies et al., 2024; Schmiedel et al., 2016), and with recent work highlighting how geomorphic and biophysical context mediates heuweltjie ecosystem engineering (McAuliffe et al., 2019). This context dependence necessitates validation of indicators rather than reliance on regional averages (Stokes et al., 2009). Paired vegetation-soil studies in the Worcester-Robertson valley and classic surveys near Clanwilliam established robust on/off-mound floristic contrasts linked to edaphic differences, which is an essential mechanistic basis for indicator development (Midgley & Musil, 1990). The broader dryland literature explains why these patch-matrix contrasts are informative for degradation diagnostics: The high degree of resource heterogeneity causes nutrients and water to become highly localized, leading to the formation of fertility islands (Schlesinger et al., 1996). Analyses that separately evaluate different mound zones (center, fringe, and matrix) consistently reveal trends (e.g., elevated soil pH and shifts in life-forms toward annuals near mound centers) (Schmiedel et al. 2016). These patterns are enhanced under heavier grazing and directly translate into potential indicator components such as the annual-perennial balance and cover structure (Schmiedel et al. 2016). Since heuweltjies are abundant and easily located, they provide repeatable, within-paddock contrasts that control for climate and land-use history. The mound–matrix couplet enables one to read management signals from **differences** rather than absolute values, thereby mitigating regional species turnover and emphasizing functional responses (palatability-weighted abundance/cover, annual proportion, growth-form structure, and plant size) that managers already use when evaluating forage (Du Toit, 2000). This study, therefore, investigates the specific ecological and structural attributes of heuweltjies, including palatable plant count, annual plant proportion, and life-form structure to determine their effectiveness as reliable indicators for assessing veld condition and informing the sustainable management of grazing capacities in semi-arid regions with winter rainfall. Specifically, we asked whether (i) palatable plants are more abundant and/or have greater cover on mounds than in the adjacent matrix; (ii) species richness and Shannon diversity differ by habitat and growth form; (iii) life-form structure (annuals vs. perennials; shrubs, grasses, herbs, succulents) shifts predictably between habitats; (iv) plant size (length/height and width) differs across growth forms by habitat; and (v) species composition separates between habitats with diagnosable indicator taxa. This study converts the well-known mound–matrix contrast into a set of repeatable, operational diagnostics (i.e., palatable counts and life-form shifts) that are directly interpretable for assessing veld condition and forage utilization.

2. Materials and Methods

2.1. Study area

The study was conducted in the Ebenhaeser communal rangelands on South Africa's West Coast, a contiguous unit located on the lower Olifants River, ~55 km from Vredendal, that encompasses the villages of Ebenhaeser and Papendorp. The area is rural, river-dependent, and closely linked to the Olifants River estuary, as well as small-scale farming and fisheries. The landscape falls within the Succulent Karoo, a semi-arid, predominantly winter-rainfall biome. Mean annual precipitation lies roughly in the 100–200 mm range with cool, wet winters and warm, dry summers. This climatic setting underpins high local endemism and functional diversity (Bell et al., 2023; Mucina et al., 2006).

Soils are shallow and heterogeneous, with aeolian sands and alluvial deposits along the lower Olifants River. Locally, these are referred to as Sandveld (aeolian) and Karooveld (alluvial). The dominant vegetation unit is Namaqualand Strandveld, characterized by shrub, and succulent-rich communities. Regional syntheses and floristic treatments place Ebenhaeser within this strandveld mosaic and allied units (Mucina et al., 2006).

The Ebenhaeser communal rangeland is situated within the broader Succulent Karoo biome (Fig. 1), where livestock grazing, particularly by sheep and goats, has been the predominant land use for several decades (Mucina et al., 2006), and where long-term grazing has been shown to produce persistent vegetation degradation and structural change (Rutherford & Powrie, 2010). Although no published ecological study has explicitly reconstructed grazing history or veld condition for Ebenhaeser at the site level, long-term studies conducted in extensively grazed rangelands within the Succulent Karoo and Namaqualand document sustained grazing pressure and persistent vegetation responses over multi-decadal timescales (Schmiedel et al., 2016; Todd & Hoffman, 1999). Within this regional context, Ebenhaeser is most appropriately interpreted as a long-utilized working rangeland rather than a lightly grazed reference system.

A conspicuous feature is the widespread presence of heuweltjies (earthen mounds) (McAuliffe, Hoffman, McFadden, Bell, et al., 2019), which form a repeating microtopographic template. Multiple studies report mound diameters of tens of metres and areal cover commonly on the order of 14 to 25% of the landscape in parts of the winter-rainfall region. This extent makes them practical reference patches for field sampling (Davids et al., 2023; McAuliffe, 2023). Within this setting, the communal rangeland (~18 000 ha) is subdivided into fenced camps that facilitate rotational grazing. Although farmers hold broadly similar total camp areas, stocking densities and strategies vary among users. This context motivates our paired mound-intermound sampling design, which allows management signals to be interpreted against a shared climatic and geomorphic backdrop.

2.2. Sampling design and field measurements

Prior to fieldwork, we met with local farmers to present objectives and obtain access permissions for camp reconnaissance. Candidate plots were mapped with a handheld GPS and Google Earth. Data were

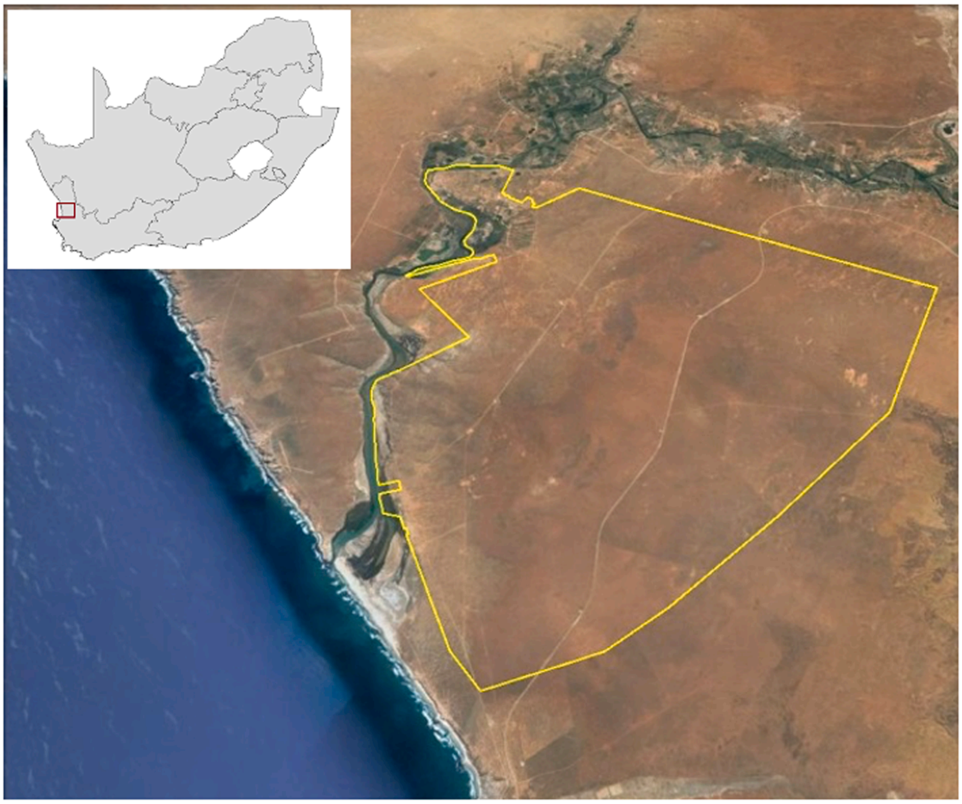

Figure 1. Study site, Ebenhaeser communal rangelands, West Coast, South Africa, indicated by the yellow border.

collected in August 2013 in three camps with the highest density of heuweltjies. We established 32 plots (5 m^2 each): 16 plots centered on mound crests and 16 paired plots in the intermound matrix, positioned at least 10 m from the nearest mound plot (Fig. 2). This created a paired design at the camp scale.

Intermound plots positioned at least 10 m from any mound. Dashed circle marks a 10 m buffer (schematic).

Within each plot, we recorded: (i) vegetation structure using the descending-point method (5 m rope marked at 1 m intervals and a measuring stick to obtain plant length/height and width at each point of contact); (ii) species composition (all vascular plants to species where possible); and (iii) species richness (plot-level S). Unidentified specimens were collected and identified using plant identification books (Le Roux et al., 2005; Manning and Goldblatt, 1996; Van der Merwe and Van Rooyen, 2010). For subsequent functional analyses, each plant record was assigned a growth form (e.g., grass, herb, leaf-succulent shrub, non-succulent shrub, stem-succulent shrub) and a life form (annual vs perennial) and scored for palatability. Each species was assigned to one of four palatability classes: 0 = unpalatable, 1 = low, 2 = medium, 3 = high. Palatability classes followed the Agricultural Research Council's

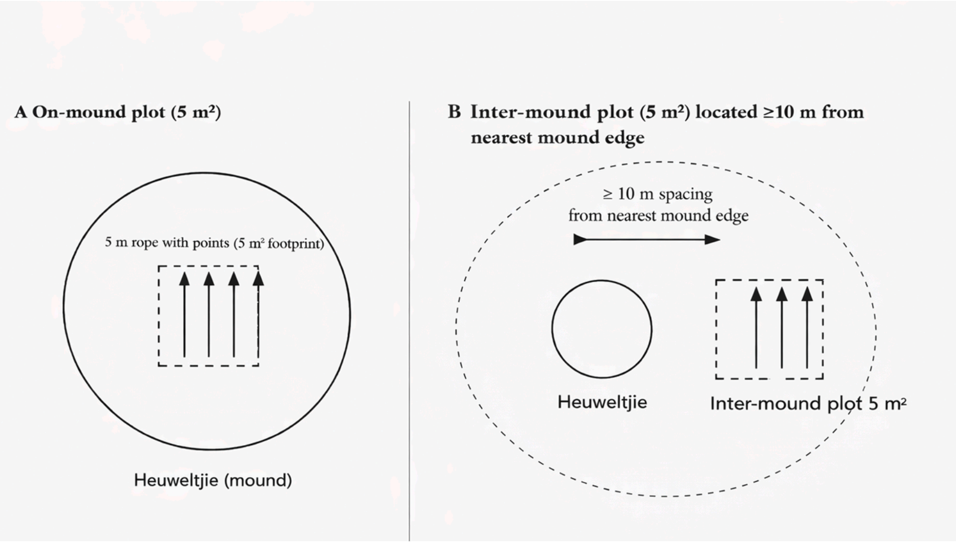

Figure 2. Schematic representation of the descending point method on the mound and in the intermound matrix. Candidate plots mapped with a handheld GPS and Google Earth.

Visual Veld Condition Assessment Tool framework and were cross-checked with local farmers' knowledge to ensure regional relevance (Barnes, 1990). Knowledge from the local farmers was used in categorising the plants that were not listed in van Breda et al. (1990).

2.3. Data preparation

All data were cleaned and standardized. Plot IDs were harmonised, and the habitat Type was recoded as Mound or Intermound. For each plant, we estimated crown cover as an ellipse: $\text{cover}_i = (\pi/4) \times \text{Length}_i \times \text{Width}_i$ in cm^2, then converted to m^2 by dividing by 10,000. Any record with a palatability class of 1 or higher was considered palatable. We then summarised the data by plot × Type (and, where relevant, by growth form or life form) to obtain: (i) total counts (individuals per plot); (ii) total cover (m^2 per plot); (iii) palatable counts and palatable cover; (iv) life-form counts/cover (annual, perennial); (v) growth-form counts/cover (grasses, herbs, leaf-succulent shrubs, non-succulent shrubs, stem-succulent shrubs); (vi) species richness (S) and Shannon diversity (H′); and (vii) the annual proportion = Annual ÷ (Annual + Perennial):

- Counts (number of individuals per plot),
- Cover (sum of individual covers, $m^2 \cdot \text{plot}^{-1}$),
- Palatable counts and palatable cover (restricted to palatable records),
- Annual and perennial counts for the annual proportion.

Species richness (S) was the number of distinct taxa per plot × Type. Shannon diversity (H′) was calculated using natural logs: $H' = -\sum p_i \ln p_i$.

2.4. Statistical analyses

The study employed a spatially explicit paired sampling design, where 16 mound plots were directly compared with 16 adjacent intermound plots, resulting in 16 paired clusters for analysis. Critically, this design means that observations within each mound–intermound pair are not statistically independent; they are spatially linked or clustered, violating the assumptions of simpler tests (e.g., standard linear models or t-tests).

We employed Generalized Estimating Equations (GEE) as the primary analytical framework. GEE, a robust extension of the Generalized Linear Model (GLM) methodology, was chosen specifically to account for the non-independence between paired plots and to provide robust, cluster-corrected standard errors (Quinn & Keough, 2002). This approach was necessary over simpler paired t-tests because the GEE framework allows us to model the diverse response variables, which include counts and proportions, often possessing non-Gaussian distributions using appropriate statistical error distributions (e.g., Poisson or Binomial) while maintaining statistical rigor for the clustered data structure. In all models, the unique identifier for each paired site (Plot ID) was designated as the clustering unit (N=16 clusters).

For continuous measures such as plant size and per-plot cover estimates, values were often right-skewed and contained zeros. To ensure that appropriate statistical assumptions were met, these response variables were log-transformed (Quinn & Keough, 2002), where a small constant was introduced to prevent undefined values for zeros. The log-transformed data were then analyzed using linear models with a Gaussian distribution.

To manage high data variability and sparsity (zero-inflation), a pre-specified analytical hierarchy was applied in cases where the primary GEE model failed to achieve reliable convergence. In such cases, models were switched to OLS (Ordinary Least Squares) regression on the log-transformed response variable. Regardless of the final model structure (GEE or OLS), Plot-clustered robust standard errors were maintained throughout the process to consistently correct for the non-independence inherent in the paired sampling design, ensuring robust inference (Quinn & Keough 2002).

Community data sparsity was addressed by conducting Principal Components Analysis (PCA) on Hellinger-transformed data (McCune and Grace, 2002). PCA visualization was complemented by an indicator-species analysis (IndVal) [Dufrêne & Legendre 1997] to identify the specific taxa driving the compositional contrasts. To mitigate the risk of Type I errors arising from multiple tests, the False Discovery Rate (FDR) control procedure (Benjamini–Hochberg) was applied to the resultant p-values.

The assumption of independence was analytically addressed through the use of the GEE/robust error structure. Furthermore, the residuals of all Generalized Linear Models were checked for spatial autocorrelation, and the normality of errors and homogeneity of variance were visually and analytically assessed for OLS approaches, following standard ecological protocols (Quinn & Keough, 2002). To systematically identify plant species associated with the paired habitat types (Mound vs. Intermound), the analysis utilized a dual statistical framework. The primary approach involved fitting a Poisson Generalized Estimating Equation (GEE) to count data for species present in both mound and intermound plots, utilizing Plot as the clustering unit to correct for the non-independence of the paired sampling design. Simultaneously, a non-parametric Indicator Species Analysis (IndVal) was conducted, which determines association through a species' specificity and fidelity to a habitat, using 499 random permutations for significance testing. This deliberate combination ensures a comprehensive result: the GEE/OLS framework provides greater statistical power and precise effect sizes by explicitly modeling the paired structure. At the same time, the assumption-free IndVal verifies the ecological association, thereby balancing statistical rigor with ecological interpretability.

3. Results

3.1. Abundance and cover of palatable plants

Across plots, palatable individuals were more abundant on mounds (rate ratio, Mound vs. Intermound ≈ = 1.54; $p = 0.012$), with a median of 7.5 palatable counts on mounds versus 5.0 on intermounds. By growth form, grasses showed a clear Type effect in abundance, favouring intermounds (median: 6.00 vs 3.00 per plot; $p < 0.001$), while herbs were enriched on mounds (median = 3, IQR 2–7) vs intermounds (median = 1, IQR 1–2; $\beta = +1.23$, $p = 0.002$) (Fig. 3).

Palatable cover was higher on mounds in direction (≈ 3.02 ×) but not significant ($p = 0.211$; Fig. 4). No growth form showed a significant Type effect in palatable cover (all $p > 0.05$).

3.2. Species richness and diversity

For most growth forms, there were no mound–intermound differences in either richness or Shannon diversity (Figs. 5 and 6). Herbs were the only growth form with a detectable signal: richness was higher on mounds (medians: 1.63 vs 1.00 species per plot; $p = 0.017$) and Shannon diversity was likewise higher on mounds (0.35 vs 0.0; $p = 0.013$). All other growth forms were non-significant for both metrics.

3.3. Life forms and annual–perennial balance

Annuals were markedly more abundant on mounds (median = 3.0 individuals vs 1.0; $p = 0.0007$) and had greater cover on mounds (medians: 0.0867 vs 0.00565 m^2 per plot; $p < 0.001$) (Fig. 7). Perennial counts and cover did not differ by Type ($p = 0.086$ and $p = 0.588$, respectively). The proportion of annuals (Annual ÷ [Annual + Perennial]) was higher on mounds, with predicted means of 0.121 on mounds vs 0.0037 on intermounds ($p < 0.001$, Fig. 8).

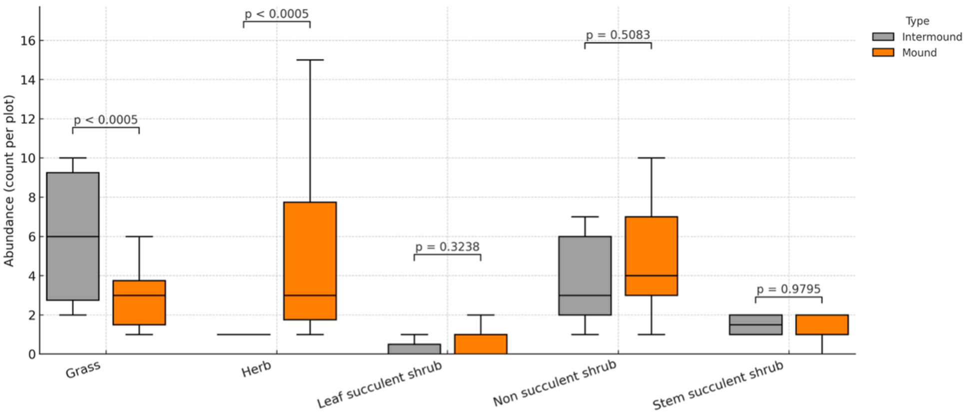

Fig. 3. Boxplots of palatable individuals for each growth form on intermounds vs mounds. The bracketed p-value is from a GEE Poisson model with Plot as the clustering unit (exchangeable correlation).

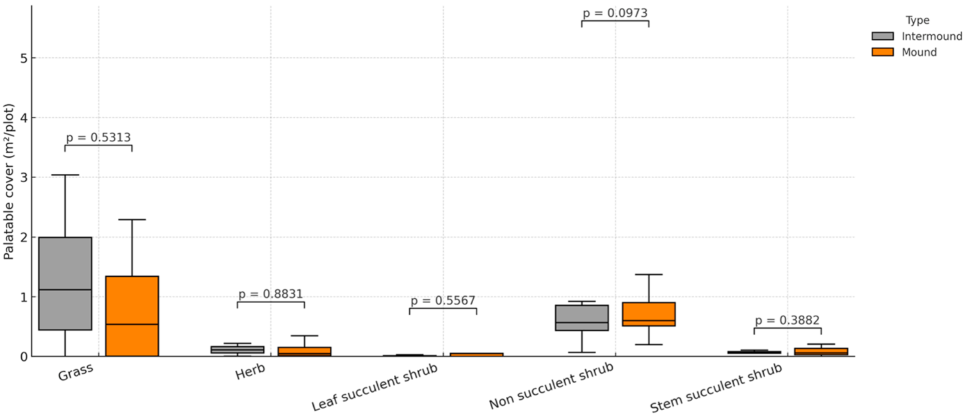

Fig. 4. Boxplots of palatable cover (m^2 per plot) for all growth forms on intermounds vs mounds. P-value from GEE Gaussian on the log scale (clustered by Plot).

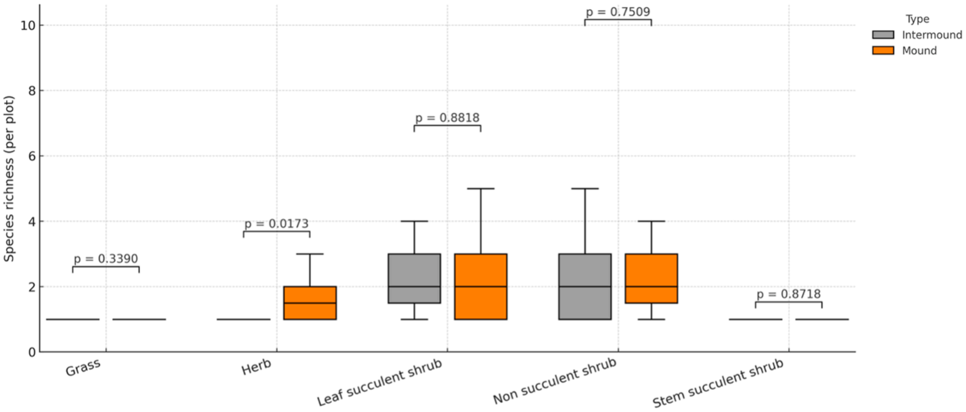

Fig. 5. Boxplots of species richness per plot within each growth form, comparing habitats. P-values from OLS on the log scale with cluster-robust SEs by Plot.

3.4. Plant size by growth form

Individuals were larger on mounds for succulent shrubs. In leaf-succulent shrubs, both length and width were greater on mounds (median length: 50.24 vs. 24.85 cm, $p < 0.001$; median width: 84.58 vs. 43.26 cm, $p < 0.001$). In stem-succulent shrubs, medium length (31.53 vs 14.17 cm; $p = 0.0030$) and median width (72.42 vs 38.00 cm; $p = 0.020$) were also greater on mounds. Other growth forms showed no significant size differences (Figs. 9 and 10).

3.5. Species composition and indicators

PCA of Hellinger-transformed plot × species cover showed a modest, consistent mound–intermound contrast: PC1 = 16.3%, PC2 = 13.3% of variance. Group ellipses overlapped, yet centroids were displaced along PC1 (intermounds higher than mounds), indicating a repeatable compositional difference. On the same Hellinger basis, a pair-restricted PERMANOVA using Euclidean distances detected a significant Type effect (pseudo-F = 2.711, $R^2 = 0.083$, $p = 0.0019$). In the biplot, the species most aligned with mounds were *Ruschia extensa* and *Asparagus*

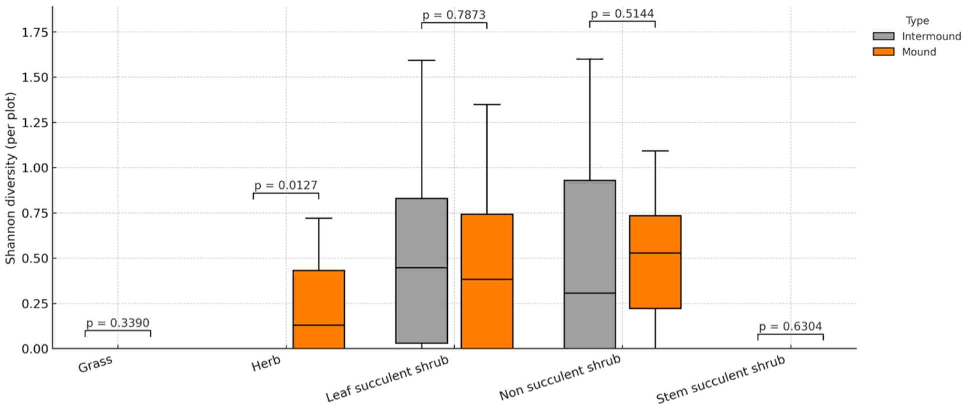

Fig. 6. Boxplots of Shannon diversity (H′) per plot within each growth form. P-values from OLS (log scale, Plot-clustered).

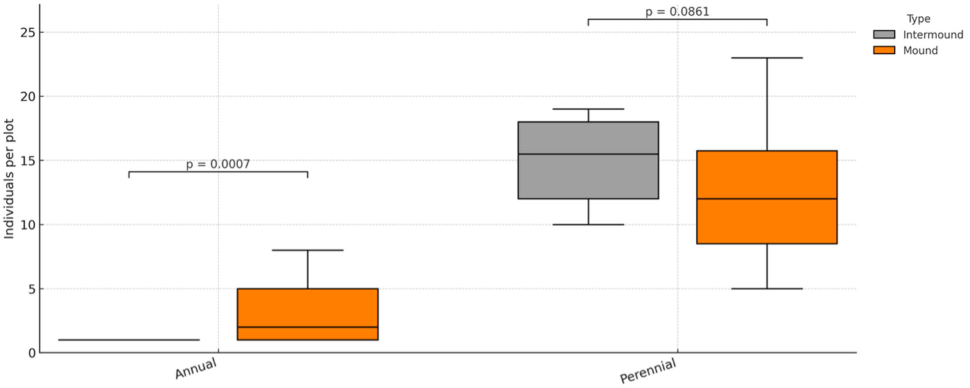

Fig. 7. Counts per plot for each life form (annual, perennial, etc.) contrasted between habitats; p-values from GEE Poisson (Plot-clustered).

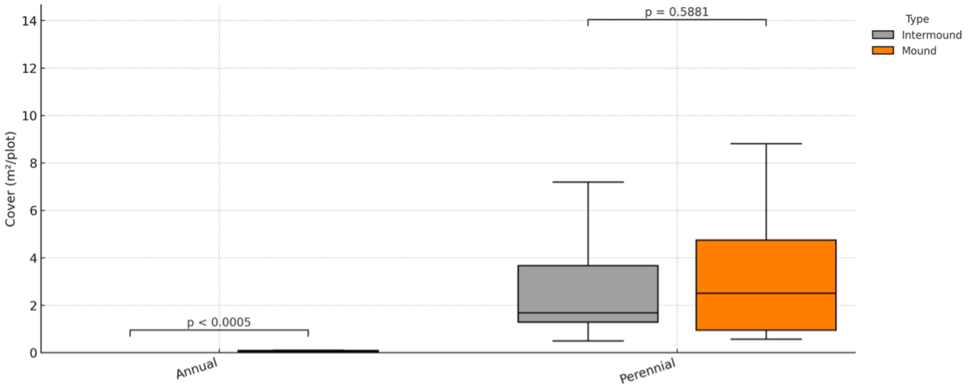

Fig.8. . Cover (m^2 per plot) for each life form contrasted between habitats; p-values from GEE Gaussian (log scale, Plot-clustered).

capensis, whereas *Ruschia sp.* and *Euphorbia karroensis* aligned with intermounds.

In the model-based indicator screen (per-species Poisson with cluster-robust SEs and FDR across testable species), 18 species yielded valid p-values, and 4 were significant at FDR 0.05. The strongest mound indicator was *Ruschia caroli* (rate ratio ≈ 3.25), and significant intermound indicators included *Ruschia* sp. 1 (RR ≈ 0.127), *Euryops* sp. 1 (RR ≈ 0.40), and *Cladoraphis spinosa* (RR ≈ 0.545). Species occurring exclusively in one habitat were flagged as type-exclusive in the table and not assigned p-values.

Indicator species results:

Model-based indicator analysis identified five robust habitat-associated taxa (FDR $q \leq 0.05$; Table S1. Four species, namely: *Ruschia sp. 1, Euryops sp. 1, Cladoraphis spinosa, and Conicosa elongata* were significantly associated with intermounds, exhibiting rate ratios between 0.13 and 0.63 (log $\beta = -2.07$ to -0.47). In contrast, *Ruschia caroli* was a strong mound indicator (log $\beta = +0.79 \pm 0.18$; RR = 2.20 [1.60–3.03]). The complementary IndVal analysis showed similar directional trends, with *Ruschia sp. 1* emerging as the strongest indicator (IndVal = 0.610; permutation p = 0.004) (Fig. 11).

4. Discussion

This study assessed whether heuweltjie mound-intermound contrasts provide field-ready indicators of veld condition and forage availability. We found higher palatable counts on mounds, a greater annual

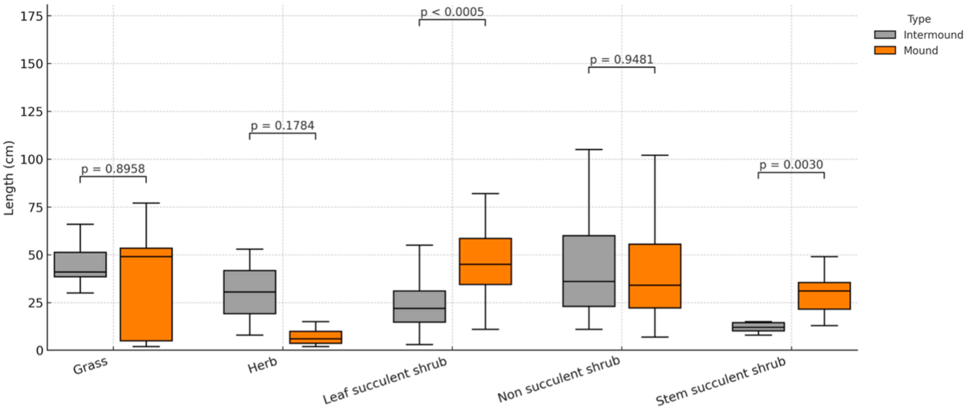

Fig. 9. Individual length (cm) contrasted between habitats within growth forms; p-values from GEE Gaussian on the log scale (Plot-clustered).

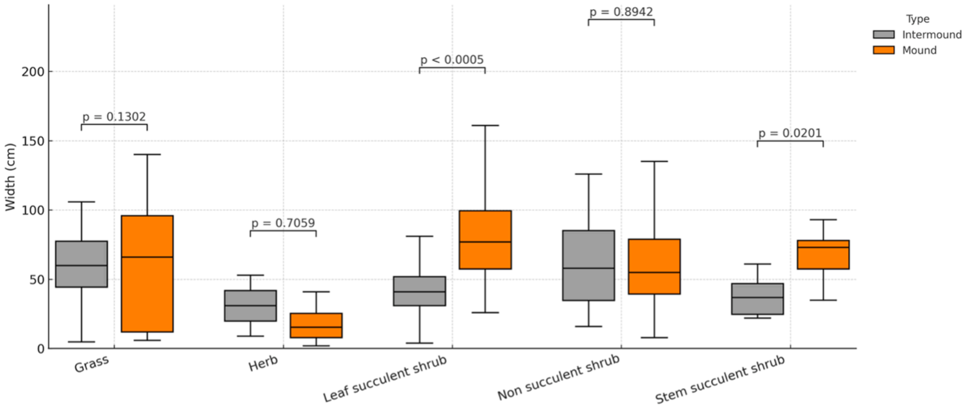

Fig. 10. Individual width (cm) contrasted between habitats within growth forms; p-values from GEE Gaussian on the log scale (Plot-clustered).

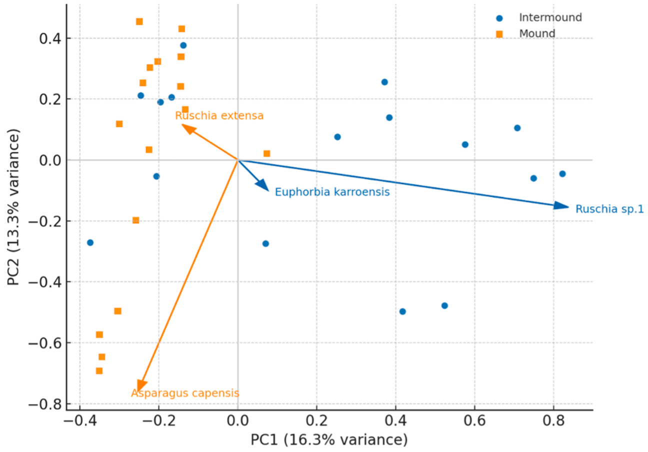

Figure 11. Ordination of 32 plots (16 mounds, 16 intermounds) based on plot-summed species cover. Covers were Hellinger-transformed and analysed by Euclidean PCA. Points are plots (Intermound = blue circles, Mound = orange squares); black "X" marks group centroids; black curves show 95% confidence ellipses around group scores; dashed lines mark axes zero. PC1 = 16.3% and PC2 = 13.3% of variance. Arrows indicate the two species most closely aligned with each habitat's direction in the PCA space (selection based on the positive projection of species loadings onto each habitat's score direction). Axis labels report the variance explained by PC1 and PC2.

proportion, larger succulent shrubs, broadly similar perennial structure, and only modest compositional separation, thus an integrated signal that translates into simple monitoring metrics. Here, we interpret the mound–intermound contrasts we observed through the lens of dryland "resource islands," local microtopography, and grazing sensitivity, and we outline how these patterns translate into operational indicators of veld condition and forage availability.

Our results showed a significantly greater abundance of palatable individuals on mounds, while palatable cover exhibited a positive but non-significant trend. This pattern aligns with the fertility hotspot concept, where enriched mound soils promote enhanced recruitment, turnover, and palatable biomass. Heuweltjie soils are typically finer-textured, more alkaline, and enriched in carbon, nitrogen, and phosphorus relative to surrounding matrix soils (Midgley & Musil, 1990). These conditions favor fast-cycling, grazing-tolerant species, even when total cover differs little (Cramer et al., 2012; Schlesinger et al., 1996). These results reaffirm that local soil heterogeneity underpins vegetation structure and shapes the distribution of palatable taxa.

At the life-form level, annuals provided the clearest management signal. They were markedly more abundant and had greater cover on mounds, whereas perennial abundance and cover showed little difference in habitat. This pattern reflects a resource-driven shift toward short-lived, pulse-responsive species that capitalize on the localized fertility and moisture of mound soils, while the perennial scaffold remains comparatively stable. Such divergence exemplifies competitive release (Noy-Meir, 1973) and mirrors semi-arid systems where heavy utilization increases annual and geophytic cover (Rutherford & Powrie, 2010). In the heuweltjieveld, the strength of mound–intermound contrasts varies along utilization gradients and across mound zones (centre → margin → matrix), with annual cover typically increasing toward mound centres under heavier grazing. This consistent annual response thus serves as a sensitive indicator of veld condition, aligning with the well-documented shrub–annual replacement under overgrazing in the

Succulent Karoo (Kunz et al., 2012).

At the growth-form level, grasses were the exception, with palatable grass counts higher on intermounds. This pattern parallels findings from savanna ecosystems, where resource availability governs competition between grasses and woody plants (Cramer et al., 2016). Grasses dominate coarser, nutrient-poor, open soils, while shrubs prevail in nutrient-rich microsites (Cramer et al., 2016). Comparable dynamics are observed in the Kruger National Park, where grass dominance is associated with nutrient-poor soils, and woody and forb cover increases on fertile termite mounds (Davies et al., 2024; Grant & Scholes, 2006; Seymour et al., 2014). These parallels highlight how interactions between soil fertility and plant competition shape vegetation patterns across African drylands. In the heuweltjieveld, grasses may prefer open intermound soils or be disadvantaged on mounds by higher alkalinity and shrub competition (Schmiedel et al., 2016). Their intermound advantage highlights that mound effects are modulated by microtopography–grazing interactions, not microtopography alone.

Species richness and Shannon diversity were broadly similar between habitats for most growth forms, with herbs the only exception (both metrics were higher on mounds). This pattern accords with global dryland syntheses, where grazing typically alters composition more than alpha diversity, and richness responses vary with aridity and productivity (Fulbright et al., 2023; Herrero-Jáuregui and Oesterheld, 2018). Stability in alpha diversity thus does not imply ecological stasis; instead, it suggests that functional and compositional metrics are better suited to capture ecological shifts. Accordingly, life-form balances provide a more sensitive monitoring tool than species counts alone, as they are more responsive to local resource enrichment and disturbance gradients (Du Toit, 2000; Schmiedel et al., 2016).

Morphometric data reinforced these contrasts. Leaf- and stem-succulent shrubs were significantly taller and wider on mounds, whereas grasses, herbs, and non-succulent shrubs showed no size differences. Larger succulent canopies on mounds indicate improved moisture retention and nutrient availability, likely linked to finer-textured soils and reduced evaporative loss (McAuliffe, 2023; Scholes et al., 2002). This size advantage supports the resource-island interpretation, where mounds maintain soil-vegetation feedbacks that sustain local productivity (Schlesinger et al., 1996). Conversely, smaller on-mound succulents or loss of size advantage may signal drought stress or heavy grazing, as high utilization is known to suppress leaf-succulent shrub cover (Riginos & Hoffman, 2003; Todd & Hoffman, 1999). Monitoring such structural attributes provides a direct, field-measurable indicator of the impact of utilization.

The indicator-species analysis yielded a concise, defensible list of taxa associated with each habitat. *Ruschia caroli* was a mound indicator, while *Ruschia sp.1* characterized intermounds. Brief indicator lists are expected when alpha diversity is stable, and habitat separation is modest, and using a formal FDR-controlled approach helps avoid over-interpretation of rare taxa. Practically, these species can be incorporated into veld monitoring protocols, complementing palatable counts and life-form balances to provide a multidimensional measure of veld condition

5. Conclusions and Implications

Three points follow from these results. First, heuweltjies provide a built-in, repeatable within-paddock control: by pairing each mound with its nearest intermound, we read management signals from differences rather than absolute values, minimizing confounding by regional turnover or between-farm history. This design advantage underpins decades of paired on- and off-mound work in heuweltjie systems (e.g., McAuliffe et al., 2014). Second, a compact indicator bundle emerges as both informative and low-cost: (i) difference in palatable count (mound-intermound), (ii) the annual proportion (typically higher on mounds under heavier use), and (iii) a grass-specific intermound check (grasses can favour the matrix), supplemented by structural safeguards on perennial parity and succulent size. Together, these capture short-term pulses (annuals, palatable counts) and longer-term structure (perennials, shrub size); their management sensitivity is supported by utilisation studies in Heuweltjieveld (Schmiedel et al., 2016). Third, stability of alpha diversity does not imply ecological stasis: modest ordination separation with a few significant indicator taxa is common where microtopography redistributes resources without overhauling the species pool, reinforcing the value of functional and morphological metrics for routine monitoring (Legendre and Gallagher, 2001).

These inferences accord with the broader islands-of-fertility paradigm in drylands, which links patch–matrix contrasts in soils and vegetation to both resilience and vulnerability under disturbance, and has long been invoked in desertification assessment (Schlesinger et al., 1996). In the heuweltjie context, syntheses and experiments emphasize that mound–matrix contrasts are long-lived yet responsive, maintained by feedbacks among vegetation, soils, and termites, and modulated by grazing. This is the combination that indicator frameworks should exploit (Cramer et al., 2012).

To operationalize the mound–intermound approach as a practical tool for veld-condition assessment or stocking guidance, three distinct steps are required. First, mound–intermound indicator differences must be calibrated against independent measures of grazing pressure or utilization (e.g., stocking density, biomass removal, or grazing history) to establish how indicator magnitude relates to veld condition. Second, soil covariates must be explicitly incorporated to distinguish grazing-driven responses from background edaphic variation, thereby improving the interpretability of indicators across heterogeneous landscapes. Third, indicator species and functional metrics must be validated across multiple sites and management contexts to assess their consistency, transferability, and sensitivity to grazing intensity. Together, these steps outline how the approach could be developed from a diagnostic framework into an applied tool for informing veld-condition assessment and management decisions (McAuliffe et al. 2014). These extensions build upon the existing literature, including paired/off-mound contrasts, grazing-interaction studies, and robust community methods (Hellinger PCA; IndVal), which already provide the analytical foundation (McAuliffe et al., 2014).

We can then conclude that, in semi-arid, winter-rainfall shrublands, heuweltjies function as built-in sensors: they concentrate palatable individuals and annuals (management-sensitive components), support larger succulents (structural condition), and subtly yet detectably register composition changes. The direction and magnitude of these mound–intermound differences, especially differences in palatable count, annual proportion, and the grass-intermound check, highlight the potential for a field-ready indicator framework. While we do not provide a final assessment of the Ebenhaeser site's absolute condition against an ungrazed benchmark, our work validates a set of candidate indicators that are theoretically grounded in fertility-island ecology and register the localized signature of utilization. By developing robust, repeatable metrics and appropriate analytical approaches, we provide the methodological foundation for future studies that calibrate these indicators against grazing intensity and veld condition across broader gradients.

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CRediT authorship contribution statement

Emilia N. Inman: Writing – original draft, Visualization, Software, Formal analysis. **Igshaan Samuels:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Clement Cupido:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Data curation, Conceptualization. **Luke Gallant:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

We have no competing interests to declare

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.sajb.2026.01.042.

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