



# Diverging responses of taxonomic, functional, and phylogenetic plant diversity to biogeographic parameters in arid habitat islands of southern Africa

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**Editors** Marcus Vinicius Cianciaruso

**Received** 19 August 2025 ♦ **Accepted** 27 January 2026 ♦ **Published** 18 February 2026

## Abstract

Habitat islands conceptually bridge true islands and habitat patches, adding new perspectives to island biogeographic principles that shape community assembly processes. Despite growing interest, empirical studies are scarce and the drivers of biodiversity in these systems, such as different aspects of island shape, isolation and habitat diversity, remain unclear. Our aim was to assess how biogeographic parameters influence taxonomic, functional, and phylogenetic plant diversity on habitat islands using quartz islands in South Africa as our model system. We conducted floristic surveys on 20 quartz islands in the harsh and arid summer-rainfall region around Pofadder (Nama-Karoo, South Africa) to quantify species richness, functional dispersion, and phylogenetic mean pairwise distance. Via remote sensing, we derived island metrics and evaluated their effects on the diversity metrics, using multivariate regression analysis. We fitted negative binomial generalized linear models for species richness and linear models for functional and phylogenetic diversity. Island area emerged as the strongest predictor of species richness, consistent with island biogeographic theory. Connectivity was a significant predictor for functional dispersion and explained most of the variation. The mean pairwise distance was significantly influenced solely by the area of the nearest neighbour island, although its explanatory power was only moderate. Our findings highlight that different facets of diversity respond distinctively to biogeographic parameters. Integrating taxonomic, functional, and phylogenetic perspectives is therefore

essential for a comprehensive understanding of biodiversity patterns on habitat islands and for providing valuable insights for conservation.

## Highlights

- First biogeographic assessment of quartz habitat islands in a summer-rainfall region: 220 vascular plant species were recorded in the Pofadder archipelago (Asteraceae, Aizoaceae and Poaceae most species-rich), and functional traits were measured for 134 perennial species.
- Species richness increased with island area (aligning with classic island biogeography) and decreased with increasing shape complexity.
- Functional and phylogenetic diversity varied little among islands, suggesting strong environmental filtering and broadly similar community composition on quartz islands.
- Functional diversity was significantly structured by island connectivity, whereas island area showed no detectable effect, potentially explained by trait redundancy in species-rich communities; phylogenetic diversity showed little response to biogeographic parameters.
- Divergent responses across taxonomic, functional and phylogenetic facets highlight the need for multidimensional biodiversity assessments in habitat islands.

## Keywords

Diversity metrics, dryland ecology, edaphic habitats, functional traits, island biogeography, island size, isolation, Nama-Karoo, quartz islands, South Africa

## Introduction

Although originally developed for true islands, the equilibrium theory of island biogeography (ETIB, MacArthur and Wilson 1967) can also act as a valuable basic concept for habitat islands (Laurance 2008), which are spatially separated habitats distinct from the surrounding matrix (Whittaker and Fernández-Palacios 2007). Several types of habitat islands have been studied, including mountain tops (Lian et al. 2025), fog oases (Gonzales et al. 2023), steppe islands (Dembicz et al. 2020), and inselbergs (Sabino et al. 2025). Unlike true islands, the terrestrial matrix is not fully uninhabitable; while acting as a strong barrier for some habitat island species (e.g. specialists), it allows others (e.g. generalists) to persist, leading to taxon-dependent permeability (Matthews 2021). In most habitat islands there is no true mainland, and the matrix can partially act as a species source (Itescu 2019). The matrix thus functions simultaneously as isolation barrier, partial mainland substitute, and driver of diversity via edge effects (Itescu 2019; Matthews 2021).

Historically, studies usually only assessed taxonomic diversity to test island size and isolation effects (Itescu 2019; Matthews 2021). However, focusing solely on species richness overlooks functional composition and trait-based environmental filtering (Cadotte et al. 2011; Garnier et al. 2016). In recent decades, many studies have moved beyond purely taxonomic approaches, incorporating functional diversity (FD) and phylogenetic diversity (PD) to capture other biodiversity dimensions and drivers (Cadotte et al. 2019; Cheng et al. 2025; Villa et al. 2025). Integrating PD and FD improves our understanding of the interplay between competition and environmental filtering in community assembly, although these metrics alone may still not fully disentangle how biotic and abiotic processes shape diversity patterns. Previous large-scale analyses of vegetation plot datasets have demonstrated that phylogenetic and functional diversity are frequently decoupled, contrary to the traditional expectation that closely related species should share similar traits (Večeřa et al. 2023; Hähn et al. 2025). This decoupling indicates that different ecological and historical assembly processes can shape these two dimensions of diversity. Functional traits may be evolutionarily labile or convergent, and FD depends strongly on the subset of traits considered, whereas PD reflects deeper lineage history and the regional evolutionary pool (Hähn et al. 2025). For example, historical dynamics such as in past refugial areas may have maintained multiple evolutionary lineages and thus preserved high PD, whereas strong and persistent environmental filtering simultaneously reduced FD via trait convergence.

Conversely, a limited set of lineages might have diversified functionally in situ, increasing FD without a comparable rise in PD (Večeřa et al. 2023). Consequently, many researchers advocate for integrating multiple dimensions of diversity to gain a more comprehensive and multifaceted picture of ecological systems (Marcantonio et al. 2014; Cadotte et al. 2019; de Bello et al. 2021b).

Nevertheless, the number of studies on habitat islands taking phylogenetic and functional diversity in addition to taxonomic diversity is still very limited (Matthews 2021). While the effects of environmental variables on plant diversity in specialized habitats have been studied in several systems (Delhay et al. 2024; Cheng et al. 2025), the influence of island biogeographic attributes remains understudied. Beyond isolation and size, factors such as matrix characteristics, edge effects, land use and habitat diversity can strongly influence species assembly (Laurance 2008; Hortal et al. 2009; Fahrig 2013; Eibes et al. 2025).

Eibes et al. (2025) showed the importance of various biogeographic factors on taxonomic diversity for quartz islands in the winter-rainfall-dominated Knersvlakte (South Africa). Quartz islands are a unique example of edaphic habitat islands (Eibes et al. 2022), characterized by a dense cover of angular quartz gravel (Schmiedel and Jürgens 1999), sharp boundaries with the matrix (Schmiedel et al. 2015; Eibes et al. 2021) and their distinct vegetation (Schmiedel 2004). They support a high diversity of endemic quartz specialists (Schmiedel 2004; Eibes et al. 2022), which evolved via in-situ speciation on quartz islands (Ellis and Weis 2006; Boucher et al. 2024; Zhigila et al. 2024). This parallels patterns observed on true islands, where high rates of endemism are a typical phenomenon (MacArthur and Wilson 1967; Kier et al. 2009).

Quartz islands can be found in several biomes such as Fynbos, Succulent Karoo and Nama-Karoo across South Africa and southern Namibia covering a broad bioclimatic gradient (Schmiedel 2004; Schmiedel and Mucina 2006; Curtis et al. 2013). The Pofadder region is, together with the Namibian Warmbad region, the only quartz island archipelago located within the summer-rainfall zone of the Nama-Karoo biome (Schmiedel 2002, 2004). Whereas the winter-rainfall region is dominated by widespread gentle showers and coastal fog, summer rainfall comes in localized thunderstorms, is highly variable, and less predictable, leading to different requirements for plants (Desmet and Cowling 1999; Mucina et al. 2006b). While the Succulent Karoo biome (in the winter-rainfall zone) shows a high plant diversity, dominated by dwarf to low-growing leaf-succulent shrubs, the Nama-Karoo biome (mainly summer rainfall) generally has lower species richness and lacks the dominance of leaf succulents (Cowling et al. 1998).

Previous studies have mostly focused on the quartz islands in the winter-rainfall or transition zone (Schmiedel and Jürgens 1999; Schmiedel and Mucina 2006; Curtis et al. 2013; Schmiedel et al. 2015; Eibes et al. 2022, 2025; Zhigila et al. 2024). However, few studies have examined quartz islands in the summer-rainfall region (Schmiedel 2002, 2004), and research on these systems remains

scarce, with only limited ongoing work (Meyer et al. 2026). These quartz islands show a relatively species- and succulent-rich vegetation (comparable to the Succulent Karoo) within the Nama–Karoo biome (Mucina et al. 2006b), making it of considerable ecological interest. Our aim is to use this terrestrial island system to expand the limited knowledge about the role of various biogeographic parameters for different aspects of plant diversity on habitat islands. We postulate the following hypotheses:

- i. Taxonomic diversity is expected to increase with island area and habitat diversity, as larger islands provide more space and different habitats, facilitating the coexistence of more species (MacArthur and Wilson 1967; Matthews 2021). In contrast, greater isolation is likely to reduce species richness by limiting the arrival of potential colonizers (MacArthur and Wilson 1967; Matthews 2021).
- ii. Functional diversity is predicted to increase with island area as well as habitat richness, as larger and more diverse islands can accommodate more species with a broader range of traits, thereby expanding the functional trait space (Ferreira-Arruda et al. 2022; Schrader et al. 2024). However, competitive exclusion could prevent functionally similar species from co-occurring on small islands, shifting the pattern toward functional overdispersion (Zhang et al. 2023). Isolation is expected to shape functional assembly of islands (Ottaviani et al. 2020) by limiting their colonization (Negoita et al. 2016). This could lead to clustering in the functional trait space on more isolated quartz islands if functional traits correlate with dispersal abilities. In contrast, traits only slightly connected (e.g. plant height) or not related to dispersal (describing leaves, epidermis and succulence) may not deviate from functional randomness with respect to isolation.
- iii. We expect two alternative patterns for phylogenetic diversity. First, if the traits driving functional diversity are phylogenetically conserved, phylogenetic diversity should respond similarly, increasing with island area and habitat diversity, but decreasing with increasing isolation due to phylogenetic clustering (Carvajal-Endara et al. 2017; Matthews et al. 2020; Kim and Lee 2021). Second, if trait divergence has occurred mainly within a small set of lineages via in-situ functional diversification, functional and phylogenetic diversity may become decoupled and exhibit different relationships with area, habitat diversity, and isolation (Večeřa et al. 2023).

Bushmanland–Warmbad phytocorion (Schmiedel 2002, 2004). It lies within one of the hottest areas in southern Africa, with mean monthly maximum temperatures reaching up to 38.3 °C during the summer months. In contrast, winter conditions can be quite cold, with mean monthly minimum temperatures dropping to as low as -0.6 °C (Mucina et al. 2006b). The climate is hyper-arid, with an extremely low average annual precipitation of approximately 92.7 mm (Desmet and Cowling 1999). Rainfall primarily occurs in the form of highly unpredictable summer thunderstorms concentrated between January and May (Desmet and Cowling 1999; Roffe et al. 2021).

The Pofadder region is situated within the Nama–Karoo biome (Rutherford and Westfall 1986) and belongs to the Palaeotropical Floristic Kingdom, in contrast to the Succulent Karoo which is part of the Cape Floristic Kingdom (Jürgens 1991). The broader vegetation matrix around Pofadder is classified mostly as Bushmanland Arid Grassland, a semi-desert steppe dominated by grass species of *Stipagrostis*, locally interspersed with low shrubs such as *Salsola* (Mucina et al. 2006b). Quartz islands are a remarkable feature of the region (Fig. 1b), which are covered with angulated quartz pebbles and dominated by low-growing succulent species (Schmiedel 2004, for examples see Fig. 2b). These habitat islands are edaphically distinct, often characterized by low pH, high salinity, and shallow soils (Schmiedel et al. 2015; Eibes et al. 2022). However, Schmiedel (2002) found evidence suggesting that salinity may play only a minor role in the Pofadder region. Surface properties of quartz islands also differ markedly from the surroundings: the high albedo of white quartz leads up to 8 K lower near-ground temperatures than in adjacent areas (Schmiedel and Jürgens 2004). These distinctive microclimatic conditions appear to be particularly advantageous for dwarf succulents (Schmiedel and Jürgens 2004), potentially leading to the unique vegetation on quartz islands, which was described by Mucina et al. (2006a) as an exclave of the Succulent Karoo biome (termed Aggeney's Gravel Vygiveld and Bushmanland Inselberg Shrubland). The Pofadder region is the only quartz island archipelago showing a high number of hemicryptophytes alongside nano-, micro-, and megachamaephytes, which dominate in all other quartz island archipelagos (Schmiedel 2004). Moreover, the Pofadder region is a center of diversity and endemism particularly due to the quartz islands (Jürgens 1991). In the past, 16 local endemic quartz specialists have been identified for the Warmbad–Bushmanland phytocorion such as the whole genus *Dinteranthus* (e.g. *Dinteranthus vanzyllii* in Fig. 2b; Schmiedel 2004).

## Materials and methods

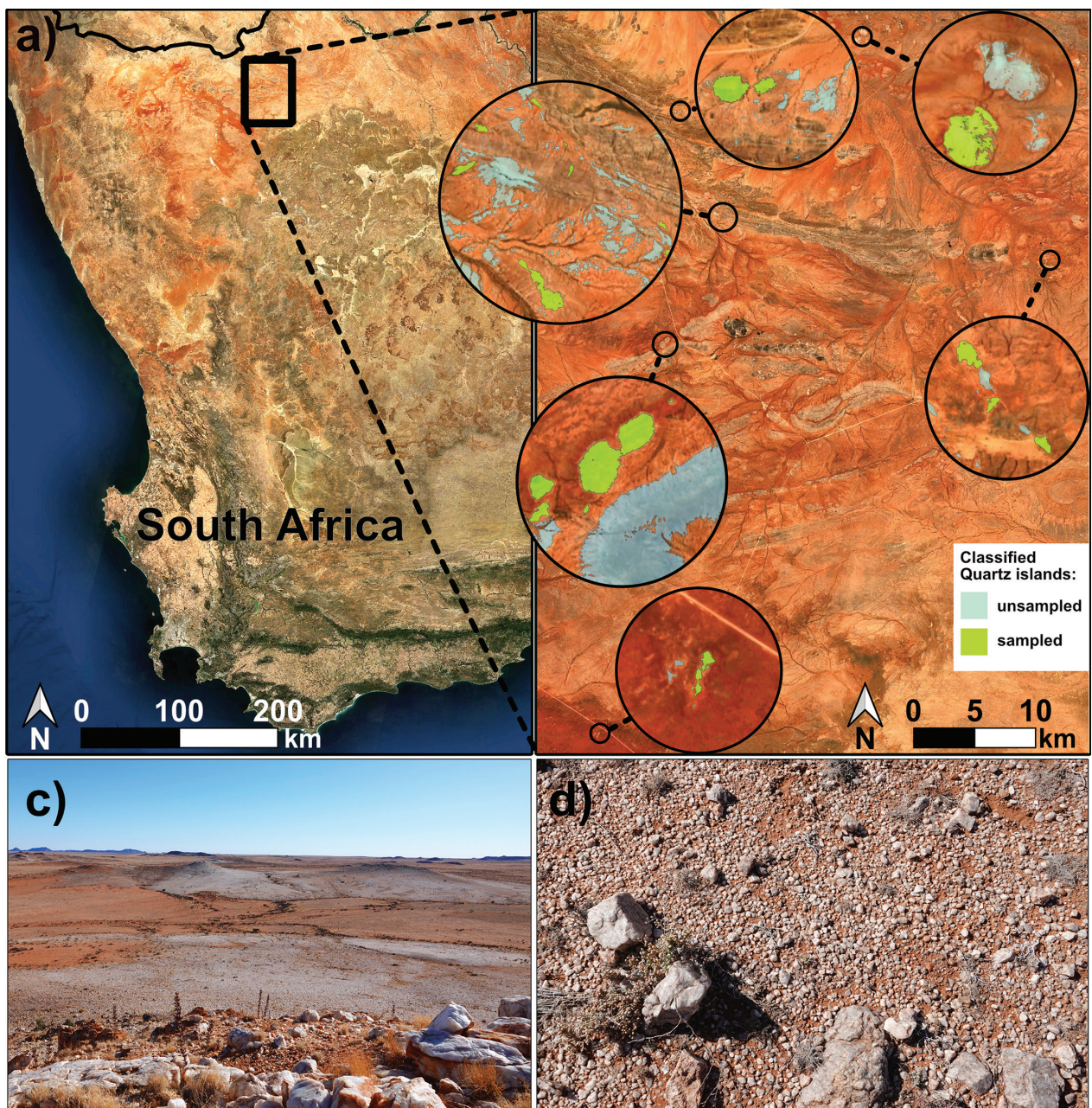
### Study area

The Pofadder region is situated in the Northern Cape Province in the northwestern part of South Africa (Fig. 1a), close to the Namibian border, and is part of the

### Data sampling

Fieldwork was conducted from February to March 2024. Species presence/absence on 20 quartz islands was assessed using systematic walk-through observations to ensure comprehensive species detection, and following a previous approach applied to the quartz islands





**Figure 1.** Overview of the study area. **a.** Location in the Pofadder region, South Africa; **b.** Detailed map of sites with close-ups showing quartz islands detected by our classifications (scale 1:17,500). Blue islands were not surveyed for species but were required to calculate the isolation metrics of the sampled islands; **c.** View from the top of a quartz island towards neighbour islands (© A. M. Bürger); **d.** Close-up of a quartz island soil surface with *Dinteranthus vanzylii*, *Mesembryanthemum tetragonum*, *Mesembryanthemum vaginatum*, and various Poaceae (© A. M. Bürger). Satellite images from Sentinel-2 cloudless (<https://s2maps.eu>) by EOX IT Services GmbH (contains modified Copernicus Sentinel data 2024).

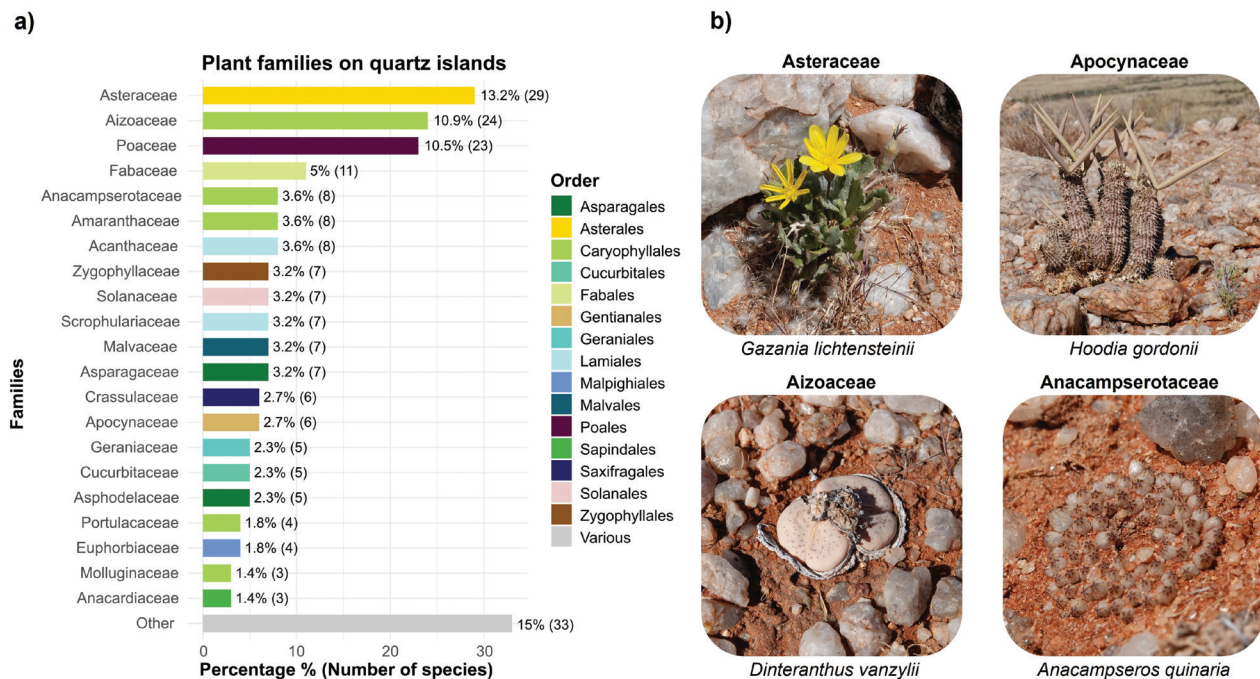
of the Knersvlakte (Eibes et al. 2025), yielding a complete species list per island. Species identification was based on relevant taxonomic literature (Suppl. material 1: table S1 for a full list of references), consultation with botanical experts, and comparison with herbarium voucher specimens (Bolus Herbarium at the University of Cape Town (**BOL**), Herbarium Hamburgense (**HBG**), and Natural History Museum Vienna (**W**)). Plant names were harmonized according to the World Checklist of Vascular Plants (Govaerts 2024) using the R package U.Taxonstand (Zhang and Qian 2023). Due to the threat

of plant poaching, particularly affecting rare and endemic dwarf succulents (Smith et al. 2023), GPS coordinates will not be published.

### Taxonomic diversity

Taxonomic diversity was quantified using species richness (SR), calculated as the total number of species recorded per island. In total, 220 vascular plant species were recorded across the 20 surveyed quartz islands (Fig. 2a).





**Figure 2.** Flora of quartz islands in the Pofadder region. **a.** Overview of quartz flora composition (220 species) by plant families on the 20 surveyed quartz islands in the Pofadder region (bar colors indicate the taxonomic order of each family); **b.** Selected plant species: *Gazania lichtensteinii*: annual generalist within the arid zone of southern Africa; *Hoodia gordonii*: leafless stem succulent; *Dinteranthus vanzylii*: dwarf leaf succulent and local quartz-endemic; and *Anacampseros quinaria*: dwarf succulent with tuberous rootstock (© A. M. Bürger).

## Functional diversity

Functional trait data were collected for 134 perennial plant species, following standard practice in trait-based ecology, prioritizing the most abundant species (de Bello et al. 2021b). Together, these species represent more than 80% of all perennial species recorded across the quartz islands. Trait measurements followed standardized protocols (Pérez-Harguindeguy et al. 2013) and adapted protocols for succulent species based on Eibes et al. (in prep.). For each species, three individuals from different locations were sampled and used to calculate functional species' trait means. For a subset of species that were locally abundant but restricted to one or a few islands, only one or two individuals could be collected; these species were also included because they provide valuable information on island-level functional diversity.

To assess functional diversity we selected the following functional traits: plant height connected to dispersal ability (Thomson et al. 2011) and representing the balance between the competitiveness of plants and adaptation to habitat harshness (Moles et al. 2009), specific leaf area indicating net primary production (Garnier et al. 2004) and negatively correlating with leaf longevity and adaptation to temperature stress (Brasil et al. 2025), leaf water content regulating leaf trait scaling relationships (Wang et al. 2022) and correlating with leaf succulence, which is an important adaptation to drought stress and arid climate (Irl et al. 2020; Pérez-López et al. 2023), and relative leaf phosphorus content as an important factor for photosynthetic rates (Walker et al. 2014). In addition, we included the presence of epidermal trichomes, prickles, wax coating, and glands, representing different strategies against

radiation, water loss, and herbivory (Hanley et al. 2007; Samuels et al. 2008; Karabourniotis et al. 2020; Tang et al. 2020) as well as stem succulence resembling adaptation to aridity (Irl et al. 2020; Pérez-López et al. 2023).

Plant height was measured in situ from ground level to the highest point of the photosynthetic tissue, excluding the inflorescence. Specific leaf area (SLA), defined as leaf area (mm<sup>2</sup>) divided by dry mass (mg), was calculated in Fiji (Schindelin et al. 2012) from scans (300 dpi) of up to 30 leaves per species using the Optical Leaf macro (Haghsheenas 2022). If highly succulent leaves resulted in scans with insufficient contrast, the leaf outlines were traced. Fresh leaf mass was determined with a precision balance. The leaves were then completely dried until their weight stabilized, and the dry mass was recorded. Relative leaf water content (%) was calculated as one minus the ratio of dry mass (mg) to fresh mass (mg). Relative leaf phosphorus content (%) was analyzed at the Department of Agriculture Western Cape Government (Elsenburg, South Africa). Stem succulence was assessed as a qualitative trait (0 = absent, 1 = moderate, 2 = strong) as well as the four-leaf epidermal traits (0 = absent, 1 = present): trichomes, prickles, wax coating and glands.

Based on these nine traits and species presence/absence per island we calculated the functional dispersion (FDis) as a measure for FD, which is considered robust to outliers and largely independent of species richness. FDis is defined as the mean distance of individual species to the centroid of the community in trait space (Laliberté and Legendre 2010). Continuous traits were log-transformed (when deviating from normal distribution) and traits were scaled to a 0–1 range to ensure independence from their individual range as

suggested by de Bello et al. (2021b). To combine quantitative and qualitative traits, a dissimilarity matrix was calculated using the Gower distance implemented in the package *gawdis* (de Bello et al. 2021a), applying optimized weighting with a group weight for the epidermal structure traits to avoid a disproportionate influence. The method handles missing values, useful for taxa lacking leaf traits, e.g., leafless *Hoodia gordonii* (Fig. 2b). FDis was calculated with the *FD* package (Laliberté et al. 2014), applying Cailliez correction for negative eigenvalues. Although FDis is often treated as independent of species richness, moderate correlations have been reported under certain conditions (Mason et al. 2013). We therefore tested for a potential richness dependency of FDis but did not detect a significant correlation, indicating that our estimates of functional dispersion were not biased by species richness (Suppl. material 1: fig. S1). Furthermore, we calculated community-mean trait values (CMs) for each island to get a better view on the functional structure of the plant communities. For quantitative traits, CMs were obtained by averaging trait values across all species present on an island. Because abundance data were unavailable, all species were weighted equally, so that each species contributed the same to the island mean irrespective of local dominance. For the categorical epidermal traits, community means were calculated as the proportion of species per island exhibiting the respective trait state. As stem succulence was recorded on an ordinal scale, we treated this trait as a numerical score. This procedure retains the ordered nature of the categories and provides an interpretable measure of average stem succulence within communities, consistent with treating ordinal intensity classes as a functional gradient.

## Phylogenetic diversity

To reconstruct a phylogeny for all recorded species, we used the *U.PhyloMaker* package (Jin and Qian 2023). We used *GBOTB.extended.WCVP.tre* megatree (Zanne et al. 2014; Smith and Brown 2018; Jin and Qian 2022) as the backbone phylogeny. The phylogeny was constructed using scenario 3 and nodes.type 1, defining how unmatched species are placed into the tree and how non-monophyletic groups are resolved (Zhang and Qian 2023). The resulting phylogenetic tree was used to calculate the mean pairwise distance (MPD) with the *mpd* function from the *picante* package (Kembel et al. 2010). The Mean Pairwise Distance (MPD) measures the average branch distance between all species pairs in a community and is widely used to quantify phylogenetic diversity (Webb et al. 2002; Tucker et al. 2017). Moreover, as a divergence measure, it is conceptual similar to FDis. We found no significant correlation between MPD and SR in our dataset (Suppl. material 1: fig. S1).

## Remote sensing data

To be able to calculate different island parameters, individual quartz islands were mapped by supervised clas-

sification of multispectral remote sensing imagery. For this, Sentinel-2 Level-2A surface reflectance imagery was retrieved with the *sen2r* R package (v 1.5-x, Ranghetti et al. 2020) selecting a single cloud-free tile (16 Dec 2023) from the Copernicus SciHub at 10 m resolution. Six sites were analyzed containing all sampled islands and their surrounding islands. Presence-only classification for quartz islands was performed with the Maximum Entropy Presence Prediction tool in SAGA-GIS (v9.1, Conrad et al. 2015) using all 12 Sentinel-2 surface-reflectance bands (10 m) and the NDVI (Tucker 1979) band as continuous predictors. Presence points were supplied to the module, whereas pseudo-absence (background) samples were drawn automatically at 0.1% of the remaining pixels across the scene. We selected the Yoshimasa Tsuruoka iterative-scaling solver (Tsuruoka et al. 2009) and applied L2 regularization with a weight of 0.01 to minimize overfitting. At two sites we switched to one-class Support Vector Machine (SVM), due to low quality of the Maxent classification. Model fitting was carried out in SAGA-GIS (v 9.1, Conrad et al. 2015) via its LIBSVM wrapper, using a sigmoid kernel. All 13 input bands were z-standardized. The regularization parameter was fixed at  $\nu = 0.5$ , allowing up to 50% of the support vectors to lie on the margin to curb overprediction (Fig. 1b). Model accuracy was evaluated against withheld ground-truth points (confusion matrix metrics: overall accuracy, producer's/user's accuracy, F-score, Kappa; Suppl. material 1: table S2). Based on the GLO-30 DEM from the Copernicus program (European Space Agency and Sinergise 2021), islands were classified into 16 distinct landform classes, including peaks, ridges, valleys, slopes, further subdivided by texture and convexity to retrieve landform data which was used to calculate habitat diversity. Using SAGA-GIS, slope and aspect were calculated with the Morphometry modules, while convexity and texture were derived using the Terrain Surface Classification module based on the algorithm by Iwahashi and Pike (2007). If classes were missing or relatively small, they were merged into the thematically closest category.

For more details see Suppl. material 1: method S1 and Oldeland et al. (2022).

## Island indices

We adapted eleven island parameters for the quartz islands of the Pofadder region based on methods described by Eibes et al. (2025). Island polygons and landform data retrieved from our quartz island classification (see remote sensing section) were loaded, transformed into a common coordinate reference system, and validated for topological correctness. Parameters describing island shape and isolation were calculated using the island polygons, whereas habitat diversity indices were derived from the landform data (slope, aspect, convexity, texture). The calculation of each parameter and the class they belong to are shown in Table 1.

**Table 1.** Biogeographic island parameters and their calculations used in this study. *i* describes the index of the targeted island. For neighbour index and proximity index a buffer with radius 1000 m was chosen to cover wind-dispersal distances (Soons et al. 2004) and to make the results comparable between the two parameters and among the different classified sites. For further information see Suppl. material 1: table S3.

Island Index	Formula	Reference
Island Shape		
Area	$A_i$	(Schrader et al. 2019) based on (Patton 1975)
Perimeter	$P_i$	
Shape Index	$\frac{P_i}{2\sqrt{\pi \cdot A_i}}$	
Distance-based Isolation		
Nearest Neighbour Distance	$\min_{j \neq i} d_{ij}$ $d_{ij}$ ...edge-to-edge-distance between islands	
5 Nearest Neighbour Mean Distance	$\frac{1}{5} \sum_k d_{ik}$ $k$ ...index of 5 nearest neighbours of island $i$	
Area-based Isolation		
Nearest Neighbour Area	$A_i, j = \arg \min_{j \neq i} d_{ij}$	
5 Nearest Neighbour Mean Area	$\frac{1}{5} \sum_k A_k$ $k$ ...index of 5 nearest neighbours of island $i$	
Connectivity-based Isolation		
Neighbour Index	$\sum_{j \in N_i}^n \frac{A_j}{(d_{ij} + 1)^2}, j \neq i$ $N_i$ ...islands within buffer around island $i$	(Kalmar and Currie 2006)
Proximity Index	$\sum_{j \in N_i}^n \frac{A_j}{d_j}, d_j = \min_{k \neq j} d_{jk}$ $N_i$ ...islands within buffer around island $i$	(Gustafson and Parker 1994)
Habitat Diversity		
Habitat Diversity Index	$\frac{TP_i}{2\sqrt{\pi \cdot A_i}}$ $TP_i$ ...Perimeter + all inner habitat edges	(Patton 1975)
Habitat Shannon Diversity	$-\sum_c p_{ic} \cdot \ln(p_{ic}), p_{ic} = \frac{A_{ic}}{A_i}$ $c$ ...different habitat classes detected on island $i$	(Shannon 1948)
Habitat Richness	$n_{ic}$ ...number of classes on island $i$	

## Statistical analysis

As an exploratory measure, relationships among diversity indices and between island parameters were quantified using Pearson's correlation coefficients (Suppl. material 1: figs S1, S2) and we used single predictor generalized linear models (GLMs) to assess the influence of island parameters on the diversity measures (Suppl. material 1: fig. S3). Right-skewed predictors were log-transformed [ $\ln(x)$ ] and all predictors z-standardized.

Prior to constructing multivariate models, we evaluated several commonly used transformations for each predictor (identity,  $\ln(x)$ ,  $x^2$  and  $x^2+x$ ). For every predictor, the transformation yielding the lowest  $AIC_c$  in a univariate LM was applied, and predictors were subsequently z-standardized. As SR is a count variable and exhibited overdispersion, we fitted a negative binomial

generalized linear model (GLM) with a log-link function (*glm.nb()*, MASS package; Venables and Ripley 2002). For FDis and MPD, Gaussian linear models (LM) were applied. Model selection was conducted with *dredge()* (*MuMIn*; Bartoń 2025), testing all predictor combinations, excluding those containing highly correlated predictors ( $|r| > 0.7$ ). Models were ranked by  $AIC_c$  and the ones with the lowest  $AIC_c$  were selected.

These final models were subjected to comprehensive diagnostic checks. Pearson residuals were plotted against fitted values to detect heteroscedasticity. For linear models, residual normality was assessed using the Shapiro–Wilk test. Influence diagnostics were performed using Cook's distance; where Cook's D indicated strong influence, we further assessed coefficient stability using HC3 heteroscedasticity-consistent standard errors (MacKinnon and White 1985) and robust

regression implemented via the packages *sandwich* (Zeileis 2004; Zeileis et al. 2020) and *lmtest* (Zeileis and Hothorn 2002). In the MPD analysis, one highly influential observation was removed and the model refitted, with robust procedures confirming the stability of the retained predictor. For the negative-binomial SR model, quality of the fit was evaluated using the overdispersion ratio and residual inspection. The standardized regression coefficients of the selected models were calculated with *parameterize()* (effectsize; Ben-Sachar et al. 2020), which were further visualized using the *ggplot2* package (Wickham 2016).

For FDis, explained variance of the best model was partitioned with *varpart()* (*vegan*; Oksanen et al. 2025). For SR, we used a pseudo- $R^2$ -based variance partitioning, following the logic of *varpart* but implemented through sequential negative binomial GLMs. No variance partitioning was performed for MPD because the best model contained only a single predictor. For all variance partitioning approaches, predictors were grouped into Island Shape, Isolation, and Habitat Diversity (see Table 1). We then modelled FDis as a function of the community mean of each trait separately to assess which traits are most strongly associated with functional dispersion. For every trait, we fitted a linear model, and a quadratic model, using standardized trait values. Linear and quadratic models were compared using a nested ANOVA and AIC; the quadratic form was retained when it improved fit ( $p < 0.05$  in the nested test or lower AIC), otherwise the linear model was selected. For the best-supported model of each trait, we recorded the coefficient of determination ( $R^2$ ) as a measure of explained variance and visualized Trait–FDis relationships. All analyses were conducted in R 4.5.0 (R Core Team 2025).

## Results

### Taxonomic diversity

Of the 220 plant species recorded on the quartz islands, roughly one third belonged to Asteraceae, Aizoaceae, or Poaceae (Fig. 2). Species richness (SR) varied strongly among islands, ranging from 23 to 105 species (mean = 54,  $sd = 23$ ), i.e. a difference of 82 species between the poorest and richest islands (Suppl. material 1: table S4). The best-supported model contained four parameters (area, shape index, nearest neighbour distance and habitat Shannon diversity, Fig. 3) and reduced the deviance in SR by about 80% relative to the null model (Fig. 4), indicating an excellent fit. There was no evidence of residual overdispersion (Pearson  $\chi^2 = 19.94$ ,  $\chi^2/df = 1.33$ ,  $p = 0.174$ ) and Pearson residuals showed no systematic pattern when plotted against fitted values, indicating that model assumptions of the negative binomial regression were met (Suppl. material 1: fig. S4a).

Partitioning of explained deviance showed that island shape (area and shape index) accounted for most

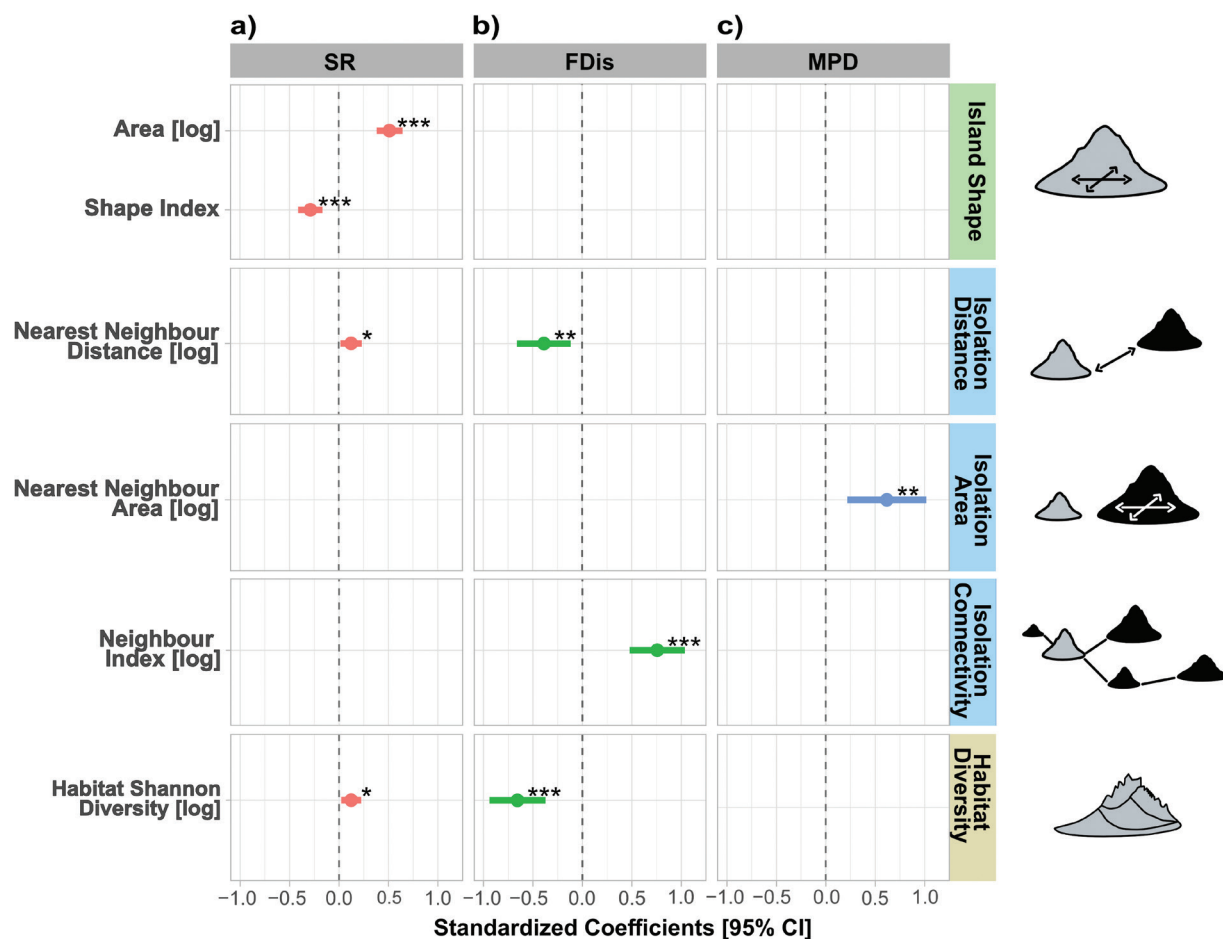
of the variation (> 80%), whereas habitat diversity and isolation jointly contributed roughly 15%, with a minor remainder attributable to shared fractions (Fig. 4). Both island area and shape index emerged as highly significant predictors of species richness, with area exerting the strongest positive effect while more irregular island shapes (higher shape index) were associated with lower SR (Fig. 3). Although shape index is derived from island area and perimeter, the correlation with area remained under the critical threshold ( $|r| < 0.7$ ). In addition to island shape effects, species richness increased with greater nearest neighbour distance and higher habitat Shannon diversity (Fig. 3).

### Functional diversity

Functional dispersion varied moderately among islands, ranging from 0.1187 to 0.1564 (mean = 0.1370,  $sd = 0.0073$ ), corresponding to a total difference of 0.0377 between the least and most functionally diverse islands (Suppl. material 1: table S4). The best-supported multi-predictor model (lowest AIC) was highly significant and explained 70% of the variation in FDis (Fig. 4). Model diagnostics indicated a good fit: residuals were normally distributed (Shapiro–Wilk  $p = 0.6284$ ) and Pearson residuals showed no systematic structure (Suppl. material 1: fig. S4b). Results were robust to influence diagnostics and HC3 heteroscedasticity-consistent standard errors (not shown). Variance partitioning revealed that isolation/connectivity metrics accounted for most of the explained variation in FDis ( $\approx 60\%$ ), whereas habitat diversity contributed the remaining part (Fig. 4). Within the multi-predictor model, island connectivity (neighbour index) exerted the strongest positive effect, while both nearest neighbour distance and habitat Shannon diversity were significantly negatively related to FDis (Fig. 3b). When relating community means (CM, Suppl. material 1: table S4) to functional dispersion, several traits showed significant associations with FDis (Suppl. material 1: fig. S5). Specifically, FDis was significantly related to the CM of SLA, leaf water content, stem succulence, as well as to the proportion of species bearing glands and prickles (all  $p < 0.05$ ;  $R^2 = 0.31–0.39$ ; Suppl. material 1: fig. S5). In contrast the CM of plant height, leaf P content, and the proportions of hairy and waxy species showed no detectable relationships with FDis ( $R^2 \leq 0.02$ ; Suppl. material 1: fig. S5).

Finally, community means varied among islands but were largely unrelated to the island parameters included in the best FDis model (Suppl. material 1: table S6). Across trait-specific models, only the CM of relative leaf water content exhibited a significant dependence on island characteristics, decreasing with increasing habitat Shannon diversity ( $p = 0.0278$ ; Suppl. material 1: table S6). All other quantitative and categorical community means showed no significant associations with nearest neighbour distance, neighbour index, or habitat diversity (Suppl. material 1: table S6).





**Figure 3.** Forest plot showing the standardized coefficients of the multivariate models with the lowest AIC assessing the effect of island parameters on different aspects of plant diversity. **a.** Species richness (SR) was fitted with a negative-binomial generalized linear model, whereas **b.** Functional dispersion (FDis) and **c.** Phylogenetic mean pairwise distance (MPD) were modelled using linear models. All island parameters were standardized. In **a**, coefficients indicate the change in species number per unit change in the predictor; in **b**, beta coefficients indicate that species are more dispersed (positive) or more clustered (negative) in functional trait space; in **c**, beta coefficients show whether species are more phylogenetically dispersed (positive) or clustered (negative). Asterisks indicate significance levels: \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

## Phylogenetic diversity

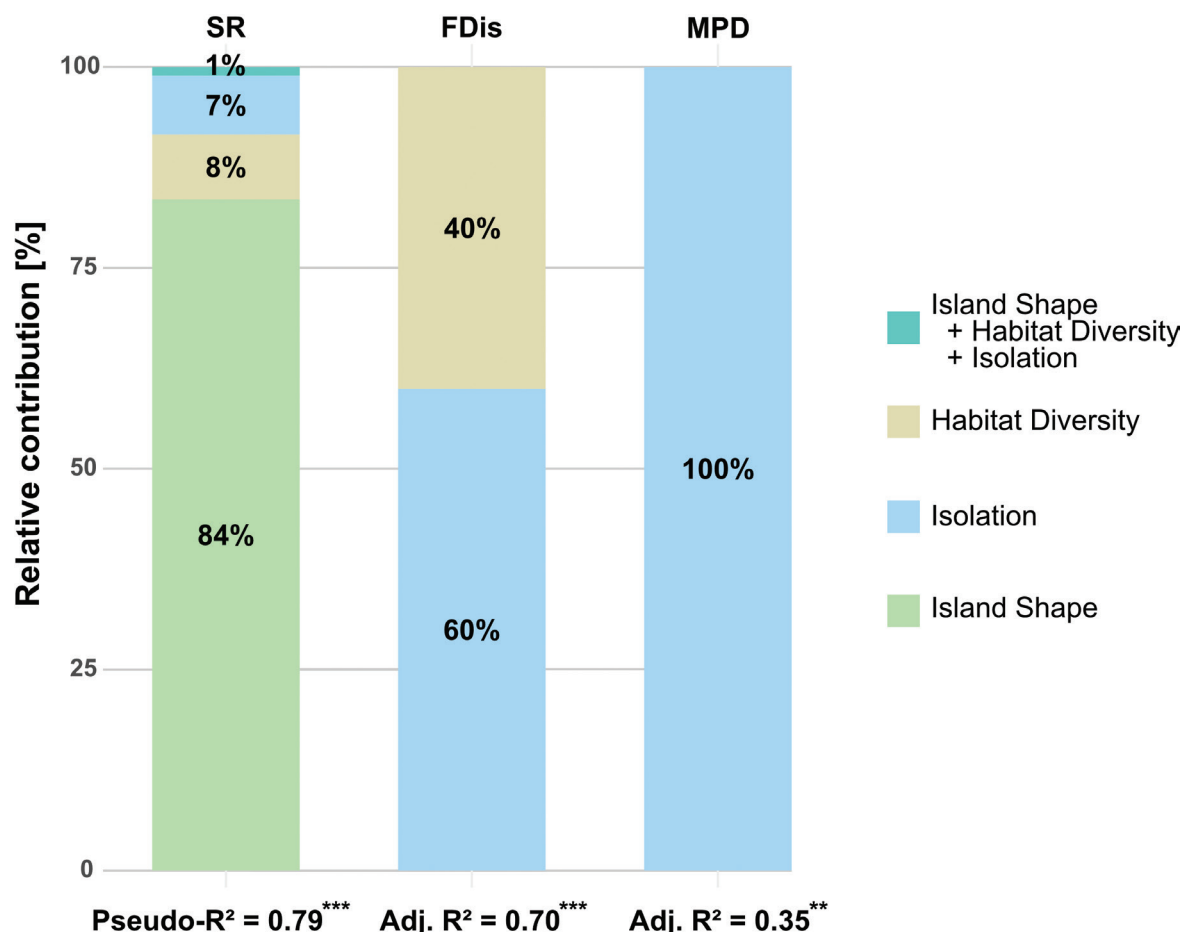
Phylogenetic mean pairwise distance varied only moderately among islands, ranging from 223.91 to 236.16 (mean = 229.37, sd = 3.42), i.e. a total difference of 12.25 units between the least and most phylogenetically dispersed islands (Suppl. material 1: table S4). Initial model selection including all islands suggested positive effects of island connectivity (neighbour index) and negative effects of nearest neighbour distance on MPD. Model diagnostics, however, indicated that one island exerted a disproportionate influence on parameter estimates. After excluding this influential island, the best-supported model retained only nearest neighbour area as a significant positive predictor of MPD (Fig. 3c). It explained about one third of the variance in MPD (Fig. 4). Residuals of the final model were approximately normally distributed (Shapiro–Wilk  $p = 0.549$ ) and Pearson residuals showed no systematic structure (Suppl. material 1: fig. S4c). Robust regression and HC3 standard errors confirmed the stability of the effect of nearest neighbour area (not shown).

## Discussion

This is the first study to quantify taxonomic, functional, and phylogenetic plant diversity on quartz islands in a summer-rainfall region. Species richness was driven primarily by island shape indices, phylogenetic mean pairwise distance was only shaped by area-based isolation, whereas functional dispersion responded to isolation and habitat diversity metrics, demonstrating diverging responses of different diversity facets to biogeographic parameters. By focusing on a quartz-island archipelago in the summer-rainfall region, which has been largely overlooked in previous research (Schmiedel 2004), our results expand our knowledge of how spatial attributes shape the diversity of habitat islands, specifically quartz islands in southern Africa.

## Taxonomic diversity

Island size showed the strongest effects on species richness (Fig. 3a), consistent with classical island



**Figure 4.** Partitioning of explained deviance (species richness) and explained variance (functional dispersion and mean pairwise distance) from the best multipredictor models (see Fig. 3). For MPD no variance partitioning was performed as the selected model had just one predictor, nevertheless it was included to complement the figure. Predictors were thematically grouped. Island Shape: area + shape index; Isolation: nearest neighbour distance nearest neighbour area, neighbour index; Habitat diversity: habitat Shannon diversity. Asterisks indicate significance levels of the models: \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ . Significance was assessed by a likelihood-ratio test for SR ( $\chi^2(4)$ : 30.74) and by an F-test for FDis ( $F_{3,16} = 15.8$ ) and MPD ( $F_{2,17} = 5.531$ ).

biogeography theory (MacArthur and Wilson 1967) and other habitat islands (Matthews 2016, 2021; Henneron et al. 2019; Mendez-Castro et al. 2021). Similar patterns were also found for quartz islands in the winter-rainfall dominated Knersvlakte (Eibes et al. 2025). Larger areas offer more resources and space, reducing the risk of population extinction (MacArthur and Wilson 1967) and have an enhanced chance of being colonized by erratic dispersal (Mendez-Castro et al. 2021). Furthermore, area correlates with habitat heterogeneity and ecological niches, increasing the potential species pool suitable for an island (Henneron et al. 2019). In addition, the shape index exhibited a significant negative effect (Fig. 3a), suggesting that high shape complexity can flatten the species–area richness relationship.

Against our expectations, isolation had a weak but significant positive effect on species richness (Fig. 3a), contrasting island biogeography theory (MacArthur and Wilson 1967; Losos and Parent 2010) and some previous works in habitat island biogeography (Dembicz et al. 2020; Matthews 2021). However, it only accounted for a small portion of the deviance explained (Fig. 4). This suggests isolation is a minor

factor for species richness on quartz islands, or that other methods may be needed to detect isolation in quartz island systems (e.g., focus on matrix effects; see Eibes et al. 2025). The minor importance of isolation is consistent with reports of weak to negligible effects in other habitat islands (Henneron et al. 2019; Liu et al. 2020) and with findings from true islands, where reported effect sizes of isolation are much smaller than those of area (Buckley 1985; Itescu et al. 2020). It would be interesting to study larger sample sizes to see if the positive effect of nearest neighbour distance persists or if it occurred because of some undetected covariations.

Moreover, habitat Shannon diversity was included in the final model (Fig. 3a), though it was based solely on topographic attributes that reflect heterogeneity rather than distinct vegetation units (Stein and Kreft 2015). Indeed, microhabitats play an important role on quartz islands, where distinct vegetation units occur in close proximity (Schmiedel and Jürgens 1999). We captured this fine scale heterogeneity using indices of topographic habitat diversity that integrate variation in slope, aspect, surface texture, and microrelief, which modulate wind exposure, solar radiation, and water availability. Although quartz islands in the

winter- and summer-rainfall regions share features such as dwarf leaf succulents and predominantly low-growing vegetation, they differ edaphically. Quartz islands in the Pofadder region differed from those in the Knersvlakte with respect to both pH and salinity, being only negligibly more acidic than the surrounding matrix and lacking an elevated salinity (Eibes et al. 2022; Lauel 2025; Meyer et al. 2026). These differences in soil conditions may be related to the regional climatic regime. The Pofadder region experiences more extreme temperatures and unpredictable heavy rainfall (Desmet and Cowling 1999). The latter can result in horizontal run-off and lateral transport of fine material and soil chemicals, thereby decreasing spatial contrasts in soil conditions between quartz islands and the surrounding matrix (Meyer et al. 2026).

In both biomes, soils on quartz islands exhibit higher edaphic aridity than the surrounding soils, generally due to their shallower soil depth, and further enhanced by increased salinity in the Succulent Karoo (Schmiedel 2015) and finer surface soil structure in the Pofadder region (Meyer et al. 2026). Despite belonging to different floristic kingdoms and biomes, the quartz floras of both regions show convergent adaptation to these arid conditions, particularly through dwarf growth forms and leaf succulence (Schmiedel and Jürgens 1999). In the Succulent Karoo, Aizoaceae have been particularly successful due to pre-adaptation to arid conditions, which, in combination with their range-restricted dispersal mechanisms, has led to rapid radiation (Klak et al. 2004). Accordingly, quartz islands in the Knersvlakte are dominated by Aizoaceae: they account for about 40% of the species pool, and together with Asteraceae and Crassulaceae they represent roughly two thirds of all species (Eibes et al. 2022).

In the Pofadder region, Aizoaceae are also well represented on quartz islands, but are clearly less dominant than in the Succulent Karoo. Here, Asteraceae constitute the most frequent family, followed by Aizoaceae and Poaceae, and together these three families account for only about one third of the species pool (Fig. 2a). This difference in family composition likely reflects, first, the influence of the regional species pool from which the quartz flora is assembled (Zhigila et al. 2024), and second, the more extreme climatic regime in the summer-rainfall Nama-Karoo. Cowling et al. (1994, 1998) suggested that recurring prolonged droughts in this region act as a major constraint on leaf-succulent richness. Although leaf succulents can tolerate low but relatively regular water availability, they show high mortality during extended dry periods (Von Willert 1985). By contrast, many Poaceae species build up large soil seed banks in arid habitats (Romig et al. 2025) and often follow ephemeral life-history strategies well suited to unpredictable rainfall and droughts (Venable and Brown 1988), potentially explaining the higher proportion of grasses on quartz islands in the summer-rainfall region.

In addition, the more extreme temperatures in the Pofadder region may further contribute to the generally lower richness of leaf succulents, as experimental climate warming has caused metabolic impairment and high mortality

in southern African quartz-field succulents (Musil et al. 2009). Together, these climatic and edaphic contrasts likely result in different matrix–island dynamics between quartz islands predominantly influenced by summer versus winter rainfall. This is supported by the presence of a distinct transition zone along island boundaries in the Pofadder region (Meyer et al. 2026), that has not been observed in the Knersvlakte (Schmiedel et al. 2015; Eibes et al. 2021).

## Functional diversity

Across islands, functional dispersion varied only within a narrow range (mean  $FDis \approx 0.14$ ,  $SD \approx 0.01$ ; Fig. 3a), indicating that communities occupy a relatively compact region of trait space (Suppl. material 1: table S4). This pattern points to strong environmental filtering and broadly similar functional composition among islands. Despite the limited spread in  $FDis$ , several island characteristics still showed significant effects, suggesting that even subtle differences in trait dispersion are structured by island properties. However, unlike species richness, functional dispersion exhibited no clear positive relationship with island size (Fig. 3b). This contrasts with our expectation that larger islands with more topographically diverse habitats would provide more ecological niches and thus support higher functional diversity (Ferreira-Arruda et al. 2022; Schrader et al. 2024). A plausible explanation is that opposing processes operate on small versus large islands. On small quartz islands, competitive exclusion may promote the coexistence of species occupying markedly different trait niches, thereby increasing functional dispersion despite low species richness (Zhang et al. 2023). However, our results are more consistent with a second mechanism. Karadimou et al. (2016) and Barabás et al. (2022) argued that functional diversity does not necessarily increase with species richness because trait space can become densely occupied in species-rich communities, reducing dispersion through redundancy. In our system, this mechanism is supported by the narrow range of  $FDis$  values across islands, which indicates that most communities share a similar set of trait combinations; additional species occurring on larger islands are therefore likely to be functionally redundant rather than expanding the occupied trait space. High levels of functional redundancy have likewise been reported for the Knersvlakte (Cowling et al. 1994). Thus, while we anticipated a significant positive area– $FDis$  relationship, our findings highlight that strong environmental filtering and trait redundancy on larger islands can decouple functional diversity from species richness on quartz islands.

Habitat Shannon diversity showed a significant negative effect in the multiple regression model (Fig. 3b), accounting for about 40% of the explained variance in functional dispersion (Fig. 4). Similar negative heterogeneity effects have been reported for Frisian islands after disentangling heterogeneity from area (Ferreira-Arruda et al. 2022) and interpreted via the area–heterogeneity trade-off (Allouche



et al. 2012), whereby higher habitat heterogeneity on small areas reduces effective habitat per species and increases extinction risk. Isolation/connectivity parameters contributed the remaining ~60% of explained variance (Fig. 4). In the multi-predictor model, the neighbour index had a strong positive effect, while nearest neighbour distance showed a weaker but significant negative effect (Fig. 3b). Higher neighbour index values indicate that surrounding islands are, on average, larger and more closely spaced, implying greater connectivity. Notably, functional dispersion showed no purely random pattern but depended on isolation despite plant height being the only trait in our dataset loosely linked to dispersal ability, and community-mean plant height showing no significant relationship with the isolation metrics (Suppl. material 1: table S6). This suggests that isolation effects on FDis are not driven by directional filtering of dispersal-related trait values captured by our trait set. Musker et al. (2021) similarly showed that spatial genetic structure and gene flow patterns in contrasting growth forms do not follow simple expectations based on plant size alone, indicating that plant height is a poor proxy for dispersal ability in this system. In addition, most species in our dataset are relatively low-growing (< 1 m), so height differences are not very pronounced. The positive connectivity effect therefore likely reflects broader assembly constraints: better-connected island systems may maintain higher functional dispersion due to more effective coupling to the regional species pool, increasing the likelihood of a more complete filling of functional niches (Baguette et al. 2013). This may be particularly important in environmentally extreme, specialist-dominated habitats such as quartz islands, where only a limited subset of the regional flora can be established.

Trait-based analyses indicate that FDis is primarily associated with community means of leaf water content, SLA, and stem succulence—traits linked to stress tolerance and resource-use strategies in arid, low-productivity environments—as well as with the epidermal traits prickles and glands, which relate to defense against biotic interactions (Suppl. material 1: fig. S5). In contrast, plant height, relative leaf phosphorus content, and the remaining epidermal traits showed no detectable relationships with FDis. Hump-shaped relationships between community mean traits and functional diversity are often reported, reflecting reduced dispersion when communities are dominated by extreme trait values (Dias et al. 2013). In our system, however, only epidermal glands and stem succulence showed this pattern, whereas the remaining traits exhibited either U-shaped relationships or no detectable associations with FDis. Because abundance data were unavailable, unweighted community means were calculated from presence–absence data. Incorporating abundance information may modify CM–FDis relationships by accounting for species dominance.

## Phylogenetic diversity

Like FDis, MPD varied only moderately across islands (Suppl. material 1: table S4). In contrast to FDis, the best

MPD model explained only about one third of the variation, with the area of the nearest neighbour island as the only significant positive predictor (Fig. 3c), while all other isolation metrics had no detectable effect (Fig. 4). Although the megatree used to derive phylogenetic distances is unresolved at the species level for parts of our dataset, MPD is considered robust to such resolution limits (Qian and Jin 2021), so this is unlikely to bias the main pattern.

This suggests that phylogenetic diversity is primarily shaped by the immediate size of the closest potential source area, rather than by broader network connectivity, as suggested for FDis. The absence of stronger isolation signals is in line with studies on other habitat island systems showing weak or random PD–insularity relationships (Klimeš et al. 2024; Sabino et al. 2025). Findings of Zhigila et al. (2024) indicate that quartz communities were originally assembled from preadapted lineages in the surrounding flora, followed by in-situ diversification on the edaphic islands. However, the floristic similarity to the Succulent Karoo and the enclave-like character of the quartz islands within the Nama–Karoo could also reflect palaeoclimatic oscillations that shifted rainfall regimes and the historical distribution of the Succulent Karoo biome (Schmiedel 2002). Under this scenario, the present-day quartz flora in the summer-rainfall region would represent a relict assemblage, with subsequent in-situ diversification and renewed environmental filtering potentially promoting functional–phylogenetic decoupling.

Overall, our data are not sufficient to support a clear pattern of either coupling or decoupling between FD and PD, unlike the distinct decoupling patterns reported at broader spatial and ecological scales (Večeřa et al. 2023; Hähn et al. 2025). Considering the univariate models, isolation metrics showed weak, non-significant, and partly opposing tendencies for FDis versus MPD, whereas both indices responded in similar directions to island shape and habitat diversity (Suppl. material 1: fig. S3). In addition, FDis was more sensitive to island parameters, yielding a better-fitting model than MPD. These patterns indicate differences between functional and phylogenetic diversity, but further studies are needed to unravel the assembly processes and mechanistic links between them.

## Conclusion

Quartz islands in South Africa represent a unique and understudied habitat island system that significantly contributes to the biodiversity and endemism of the Karoo (Schmiedel 2004). This study offers the first biogeographic perspective on quartz islands in the harsh, arid summer-rainfall region, applying a multifaceted approach to examine how island parameters such as area and isolation influence taxonomic, functional, and phylogenetic plant diversity. Because quartz islands occur across multiple archipelagos along a wide bioclimatic gradient, they offer an exceptional natural system for comparative habitat island biogeography. Future research should extend

taxonomic, functional and phylogenetic diversity analyses across regions on a larger scale to identify their main drivers and to determine how climate shapes functional trait space and island-biogeographic relationships in otherwise comparable edaphic environments. Furthermore, it would be highly informative to connect phylogeny with functional traits in the quartz flora, to test whether certain trait classes are more phylogenetically conserved than others. This would help interpret diversity patterns and assembly processes, while help to reveal the relationship between functional and phylogenetic diversity.

Overall, our findings advance habitat-island biogeography and provide ecologically relevant insights into the functioning of species-rich quartz islands. They further highlight conservation priorities on largely privately owned land where threats such as dwarf succulent poaching persist (Smith et al. 2023). Specifically, conservation should safeguard both large islands—given the strong area effect on species richness—and well-connected networks of intact islands, which appear crucial for maintaining functional diversity. Maintaining connectivity is also likely to support dispersal and gene flow among islands (Schmidt et al. 2025), thereby enhancing the adaptive potential of quartz island floras under ongoing global change.

## Acknowledgements

We are grateful to the Department of Environment and Nature Conservation (Northern Cape, SA) for issuing the necessary research permit (permit number: FLORA 0004/2024). Our heartfelt thanks go to the farmers who generously allowed us to conduct fieldwork on their private land. Our thanks go to Sebastian Wilfinger and Fenja Wiese for their assistance in measuring functional plant traits. Special appreciation is extended to the following experts for their invaluable support in plant identification: Cornelia Klak (Aizoaceae), Peter V. Bruyns (Euphorbiaceae), and Annelise Le Roux (various taxa). Furthermore, we thank the University of Hamburg, the University of Cape Town, and the Natural History Museum of Vienna for granting us access to their herbarium collections. Lastly, we sincerely thank the handling editor, Marcus Vinicius Cianciaruso, and the two reviewers for their constructive and insightful comments, which substantially improved the manuscript. We are particularly grateful to Rafael Molina-Venegas for additional follow-up discussion during the revision process.

## Author contributions

AMB and SDHI conceived the ideas and designed methodology; AMB, KM, CL, and US collected the data; AMB, JO and SDHI analyzed the data with contributions by PME; AMB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Use of AI

OpenAI's ChatGPT assisted with language editing and provided support in code debugging and structuring.

## Funding

We sincerely thank the German Research Foundation (DFG, project number: 404519812) for funding our Quartz Island II project.

## Data availability statement

The data underpinning the analysis reported in this paper are deposited in the Dryad Data Repository at <https://doi.org/10.5061/dryad.15dv41p8x>.

## Competing interests

The authors have declared that no competing interests exist.

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## Supplementary materials

### Supplementary material 1

**Supplementary tables S1–S6, figs S1–S5 and method S1 (.docx)**

Link: <https://doi.org/10.21425/fob.19.167957.suppl1>