




Partitioned beta diversity patterns of plants across sharp and distinct boundaries of quartz habitat islands

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Abstract

Questions: Habitat islands are often characterized by the presence of more or less sharp boundaries to adjacent matrix habitats. However, knowledge on boundaries of natural habitat islands is scarce, especially regarding patterns of beta diversity and its two underlying components: species turnover and nestedness. We therefore aim to quantify the effects of fine-scaled and sharp boundaries of quartz islands (quartz gravel-covered soils) on the different components of plant beta diversity and how they are linked to different soil environmental drivers.

Location: Knersvlakte, Western Cape, South Africa.

Methods: We sampled plant species richness in 56 fine-scale transects of 6 m × 1 m plots across eight different boundary types (four quartz island to matrix, four between habitats on quartz islands). Soil depth and chemistry (pH, electrical conductivity) were analyzed for each 1 m² plot. Differences in the two beta diversity components (turnover and nestedness) for each boundary type were tested by *t* tests. We used linear models to test relationships between species and environmental dissimilarity.

Results: All boundary types showed high beta diversity. Species turnover was the prevailing component for six boundary types, the nestedness component was only important for two boundary types. We found a significant linear increase of species dissimilarity with increasing dissimilarity in soil pH and distinct plant communities for the habitat types, but no significant increase for electrical conductivity or soil depth.

Conclusions: The spatial distinctiveness of the quartz islands leads to sharp boundaries, which result in high beta diversity, mainly through species turnover. This reflects the high levels of diversification and adaptation of the local plant communities. Nestedness occurred at two boundaries to the matrix, indicating that the latter does not necessarily represent an impermeable boundary for all species of the respective ecosystem. Studying diversity patterns across boundaries contributes to the question of applicability of island biogeography theory to habitat islands.

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KEYWORDS

beta diversity, boundary dynamics, community ecology, diversity indices, ecotone, edge effects, habitat island, nestedness, quartz fields, soil diversity, species turnover, Succulent Karoo, transition zone

1 | INTRODUCTION

Sharp boundaries between natural habitats that extend over only a few centimeters are rare in natural ecosystems. Most transition zones, irrespective of geographical, environmental or temporal character, proceed over larger extents or often show stepwise or gradual intermediate stages (Strayer et al., 2003). Where sharp and small-scale habitat boundaries occur, as in the case of fragmented systems, they are mostly of anthropogenic and not of natural origin (Collinge & Forman, 2009). Small-scale boundaries usually indicate strong and abrupt changes in environmental conditions; often with a similarly abrupt biological response (e.g. represented in altered species composition; Danz et al., 2013; Schmiedel et al., 2015; Osman et al., 2019). Along steep gradients, environmental filtering represents a main process sorting plant communities by excluding those species from a site that cannot cope with its abiotic properties (Kraft et al., 2015). Just like the boundary characteristics such as sharpness and width, the prevailing environmental drivers are scale-dependent (Willis & Whittaker, 2002): Climate and macrotopography have the greatest impacts at large-scale gradients and boundaries (e.g. ecotones separating biomes or elevational gradients; Neilson, 1993), whereas local parameters such as soil acidity, salinity or depth gain in importance at the patch or community scale (Gosz, 1993; Risser, 1995). As steep environmental gradients are furthermore suggested to play an important evolutionary role through strengthening selection pressure (Moritz et al., 2000; Schilthuizen, 2000), sharp boundaries represent dynamic and reactive systems (Kark, 2013), which are highly suitable for studies on species assembly and the generation of diversity. However, studies investigating boundaries of similar small scales in arid or semi-arid environments are scarce (Rubio & Escudero, 2000).

Diversity measures are one of many methods to analyze different aspects of biodiversity across boundaries (Hufkens et al., 2009). They provide insights at different levels: local diversity (alpha diversity) describes the diversity within a certain site, regional diversity (gamma diversity) describes the diversity of a whole landscape, while beta diversity quantifies the diversity differences between certain sites (Whittaker, 1972). Following Baselga (2010), beta diversity can be partitioned into two components: turnover and nestedness (Baselga, 2010; Baselga & Orme, 2012). Both compartments contribute jointly to beta diversity, but quantifying them separately can provide inferences about underlying ecological drivers (Guo et al., 2018). Species turnover is the replacement component of species (species composition of sites differs due to species being substituted by the same number of other species) and is suggested to indicate deterministic processes related to environmental filtering. Beta diversity mainly explained by turnover implies strong control by

environmental or ecological variables and reflects that turnover occurs when species meet their ecological limits (Leprieur et al., 2011). Nestedness represents the subset or richness component (species composition of a site is a subset of another one due to species gain or loss) and implies stochastic processes related to e.g. dispersal, colonization or extinction (Guo et al., 2018). As patterns leading to species loss or gain are diverse, several explanations can underlie a high proportion of nestedness, including physical barriers for dispersal, a reduction of niche availability at different sites, selective colonization or extinction (Baselga, 2010; Leprieur et al., 2011; Legendre, 2014). Beta diversity measurements are appropriate tools to quantify shifts in species composition, commonly used in studies along environmental gradients, but also applicable to transition zones (Williams et al., 1999; Ficetola & Denoël, 2009; Kark, 2013).

Beta diversity is related to spatial heterogeneity, which is usually higher in patchy landscapes, where the mosaic-like arrangement of adjacent habitat patches with varying environmental and ecological characteristics results in a complex landscape structure (Peters et al., 2006; Tscharncke et al., 2012; Gavish et al., 2019). Beta diversity is often underestimated regarding the overall diversity of a landscape, even though it can increase gamma diversity, especially in mosaic-like landscapes (Tscharncke et al., 2012). Habitat islands, which represent such mosaic-like ecosystems, share comparable features with true islands (Itescu, 2018) and even very small natural patches can add diversity to an otherwise homogeneous landscape (Deák et al., 2021). However, there are also differences, of which the most apparent, and probably most fundamental, is the nature of the adjacent matrix. The boundary between the habitat island and matrix thus does not necessarily mean an impassable limitation for all terrestrial taxa and beta diversity partitioning might provide an initial measure of the boundary permeability for certain species. A high beta diversity between habitat island and the matrix that is mainly driven by the nestedness component therefore indicates that several species are able to occur in both the habitat island and matrix. Furthermore, spatial (width, extent), environmental (sharpness, contrast) and ecological (community assembly, species-specific niche differences) properties shape varying beta diversity patterns at this transition zone. While beta diversity patterns at transition zones of anthropogenic fragmented ecosystems have frequently been studied (often under the term edge effects), boundaries of semi-natural or natural fragmented systems are underrepresented (Erdős et al., 2019).

The Succulent Karoo is one of the main biomes in South Africa and extends over large parts in the west of the country (Mucina et al., 2006). The Knersvlakte bioregion in the Western Cape Province falls within the Succulent Karoo. Here, the quartz islands represent azonal habitat islands, which are grouped in archipelago-like systems within the zonal vegetation of the Succulent Karoo.

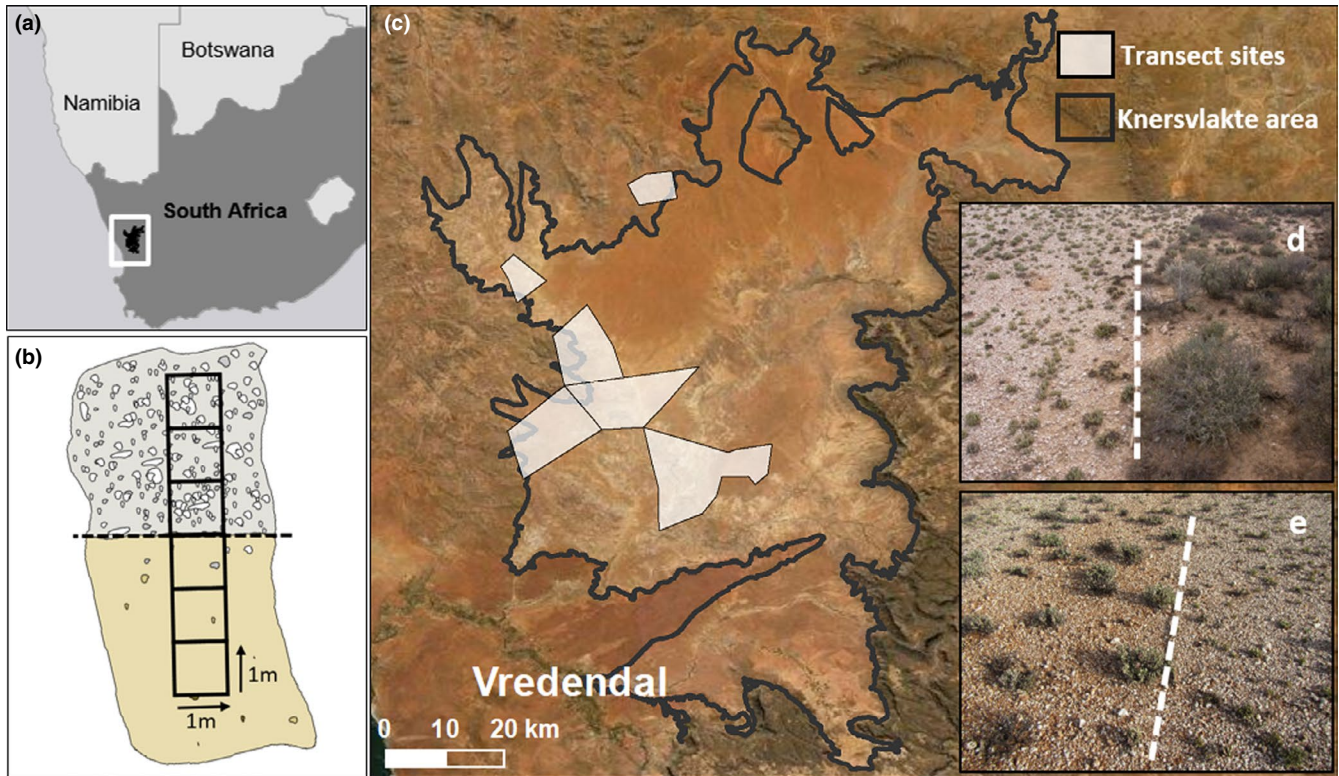


FIGURE 1 Study area: (a) The location of the study area in South Africa indicated by the black area within the white frame. (b) Sampling design with one transect consisting of $6 \text{ m} \times 1 \text{ m}$ plots placed perpendicular to the identified boundary. (c) The locations of the sampling sites within the Knersvlakte (Western Cape province) indicated by the white shaded areas. (In cooperation with the local conservation agency, CapeNature, we do not show the exact coordinates of the 56 transect positions, as the region is severely affected by plant poaching.) (d) Example of a boundary (white dashed line) between a quartz and a matrix habitat (“*Argyroderma fissum*–*Cephalophyllum spissum* to matrix,” photo: Alina Twerski). (e) Example of a boundary (white dashed line) between two quartz habitats (“*Ruschia burtoniae* to *Argyroderma fissum*–*Cephalophyllum spissum*,” photo: Nicole Kühne). (Basemap sources: Esri, Digital Globe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS user community; Shapefile of Knersvlakte provided by CapeNature)

These habitat islands are isolated units covered by whitish quartz gravel (Schmiedel & Jürgens, 1999) and are a naturally fragmented system. The Knersvlakte itself is known as a center of plant diversity and endemism (Cowling et al., 1994). The quartz islands harbor an outstanding number of plants, mainly dwarf leaf-succulents from the Aizoaceae, Asteraceae and Crassulaceae families, which are often rare or endemic species (Schmiedel & Jürgens, 1999; Mucina et al., 2006). Matrix habitats are characterized by deeper and less acidic soils and a higher share of leaf-succulent and non-succulent fruticose growth form types but by a higher abundance of annuals (Haarmeyer et al., 2010). Plant communities on quartz islands and within the zonal Succulent Karoo habitats (hereinafter: matrix habitats) thus differ in plant species and life-form type composition. But also within the quartz islands, different habitats are defined by different vegetation communities with sharp (within a few centimeters to meters of width) and distinct intra-island boundaries are easily identifiable as apparent lines in the landscape. Schmiedel et al. (2015) showed that these boundaries are driven by steep and small-scale environmental changes in the soil, mainly soil acidity and salinity, resulting in abrupt shifts in species assemblages. They found high fidelity values of certain indicator species for all included quartz and

matrix habitats, which illustrates the high habitat specialization of the local plant species of the Knersvlakte, leading to the assumption that species turnover between adjacent habitat types is high.

In this study, we investigate the patterns of partitioned beta diversity of plant communities at habitat boundaries within natural habitat islands as well as between habitat islands and the adjacent matrix. We test the following hypotheses: (a) sharp boundaries result in high beta diversity, which will be mainly explained by high species turnover compared to nestedness; (b) habitat dissimilarity of adjacent sides of the boundary increases with increasing difference in environmental parameters; and (c) intra-island boundaries show lower dissimilarity in species composition than island–matrix boundaries.

2 | METHODS

2.1 | Study area

The Knersvlakte is located in the Namaqualand within the Western Cape Province in South Africa and extends over an area

of 10,000 km² (Figure 1). The Knersvlakte belongs to the Succulent Karoo biome, which is reported as one of the 25 global hotspots of biodiversity hosting 4,849 plant species and 0.6% of the endemic plant species worldwide (Myers et al., 2000). Dwarf succulent shrubs mainly of the Aizoaceae, Crassulaceae and Asteraceae plant families dominate the local vegetation. The region is characterized by an arid winter-rainfall climate with the largest amount of rainfall during the mild winter months. The mean annual temperature ranges from 17.9°C to 18.6°C, while summer temperatures reach 30°C to 35°C (Mucina et al., 2006). A predominantly plain geomorphology with gently sloping hills characterizes the landscape of the Knersvlakte. Large parts are covered by angular whitish quartz gravel and form so-called quartz islands which are largely restricted to the Succulent Karoo (Mucina et al., 2006) and can widely differ in shape and size (ranging from few to several hundreds of meters in diameter; Schmiedel & Jürgens, 1999). The quartz islands are defined by sharp boundaries and form a distinct patchy mosaic with the adjacent zonal soil types. They are edaphically special habitats with usually very shallow soils, special soil chemistry (Schmiedel & Jürgens, 1999) and even altered microclimatic conditions such as temperature buffering by increased albedo (Schmiedel & Jürgens, 2004). Very saline and acidic soils present two extremes of soil chemical gradients that characterize the quartz island habitats. Schmiedel et al. (2015) identified soil pH, electrical conductivity and soil depth as main environmental drivers of quartz island vegetation communities.

2.2 | Sampling design

A total of 56 transects of 6 m × 1 m plots across eight different boundary types was sampled, involving four habitat types on quartz islands (salt pan, *Dicrocaulon brevifolium* habitat, *Argyroderma fissum*–*Cephalophyllum spissum* habitat, *Ruschia burtoniae* habitat) and two habitat types in the matrix (non-quartz field, Heuweltjies). Quartz habitats were named according to characteristic species or properties: *Dicrocaulon brevifolium* and *Ruschia burtoniae* represent acid quartz habitats, while *Argyroderma fissum*–*Cephalophyllum spissum* and salt pan represent saline quartz habitats (Schmiedel et al., 2015). The matrix habitat non-quartz field includes all zonal areas that are not covered with quartz gravel. Heuweltjies represent a separate azonal habitat type, but since they are not covered with quartz gravel, we grouped them together with the non-quartz fields under matrix habitats. Heuweltjies means “small hills” in Afrikaans and describes a particular slightly elevated soil structure that is common in the Knersvlakte. The origin of these structures is still under debate (McAuliffe et al., 2019), but most authors assume that they represent fossil termitaria (see Lovegrove & Siegfried, 1989; Moore & Picker, 1991; Schmiedel et al., 2015 for more detailed descriptions). Sampling design and habitat types were defined by Schmiedel et al. (2015) and are based on species composition and named after dominant species. Half of the transects were placed across boundaries from habitats on the quartz islands to the adjacent matrix habitats,

the other half was put across distinct habitat boundaries within the quartz islands. The transects consisted of 6 m × 1 m (3 m × 1 m for each respective transect side) sections and were placed perpendicular to the visually identified boundary. Soil depth (in cm) was measured at three randomly selected locations within the 1 m² plot by hammering a metal pin into the soil as far as possible. A composite soil sample was also taken at three randomly chosen sites within each 1 m² plot in the uppermost soil layer of 0–2 cm depth. This depth was chosen because the rooting depths of the majority of the plants on the quartz islands are very shallow and soil variables vary most strongly at the surface layer.

2.3 | Soil analysis

We measured soil pH by dissolving 10 g of the dried and sieved soil samples in 25 ml of 0.01 M CaCl₂. Electrical conductivity was measured by suspending 10 g of soil in 25 ml of distilled water. Both suspensions were mixed, and pH and electrical conductivity were measured after 1 hr by a multi-parameter meter with the pH electrode and electrical conductivity electrode.

2.4 | Data analysis

2.4.1 | Beta diversity, turnover and nestedness

All of the following analyses were performed in R version 4.0.2 (R Core Team, 2020). We used the R package *betapart* (Baselga & Orme, 2012) to quantify beta diversity, species turnover and nestedness of each transect, based on the presence/absence data of the species per 1 m² plot. This was done by calculating the multiple site Jaccard dissimilarity with the *beta.multi* function, which returns a value for turnover, nestedness as well as overall Jaccard dissimilarity (overall beta diversity as the sum of its two components) for each transect. Transects were then grouped according to their boundary type ($n = 8$). Differences in mean turnover and mean nestedness values within the boundary type groups were tested via pairwise Student *t* test.

2.4.2 | Environmental differences of the transect sides

For each transect ($n = 56$) we calculated the difference (delta value) in the three environmental parameters pH, electrical conductivity and soil depth. This was done by subtracting the average soil parameter value of all plots per transect that belonged to the same habitat type from the average value of the respective adjacent habitat type of the same transect. We then used linear models (LMs) to test the Jaccard dissimilarity against the difference in the three respective environmental parameters. Model assumptions were checked by plotting the histogram of the standardized residuals of each model respectively.

2.4.3 | Species composition of habitats

We performed non-metric multidimensional scaling (NMDS) based on the Jaccard dissimilarity of all transects to graphically analyze dissimilarities in species compositions of all six habitat types (four quartz island habitat types, two matrix habitat types). NMDS was calculated using the metaMDS function in the R package *vegan* (Oksanen et al., 2017); the appropriate number of dimensions was determined by plotting the stress values (considering stress values <0.1 as good fit) against the number of dimensions with the dimcheckMDS function (trymax = 100). Collinearity of environmental variables was checked by Pearson's correlation coefficient before the subsequent fitting of the significant environmental variables with the envfit function. The correlation between the environmental parameters and the first two NMDS axes was tested with the cor function. Visually interpreted differences between habitat types were subsequently tested by an analysis of similarity (ANOSIM) with the anosim function, based on the Jaccard dissimilarities of all transects (permutations = 9,999). We extracted the scores of the first and second axis of the NMDS for the six different habitat types. After testing for normal distribution of the scores, we used analysis of variance (one-way ANOVA) with a Tukey's Honest Significance Differences post hoc test (Tukey HSD) to test for differences between the habitat types along the first and second NMDS axis. We subsequently tested for differences in the environmental parameters between the habitat types by applying a Kruskal-Wallis analysis of variance with a subsequent multiple pairwise comparison by a Wilcoxon test with a Bonferroni correction for multiple testing, as environmental variables were not normally distributed.

3 | RESULTS

3.1 | Beta diversity, species turnover and nestedness

Mean Jaccard dissimilarity (overall beta diversity) was relatively high for all boundary types and ranged between 0.74 and 0.86. The turnover component was significantly higher than the nestedness component for six boundary types. For two boundary types, "*Argyroderma fissum*-*Cephalophyllum spissum* to Heuweltjies" and "salt pan to Heuweltjies," turnover and nestedness were not significantly different (Figure 2).

3.2 | Environmental differences of transect sides

The LMs revealed a significant increase in the Jaccard dissimilarity of species composition with increasing differences of the pH values of the adjacent transect sites, but the explained variance was low ($r^2 = 0.1067$, $p = 0.014$; Figure 3a, Appendix S1). The model for electric conductivity did not show a significant correlation (Figure 3b, Appendix S1), while Jaccard dissimilarity of adjacent transect sites

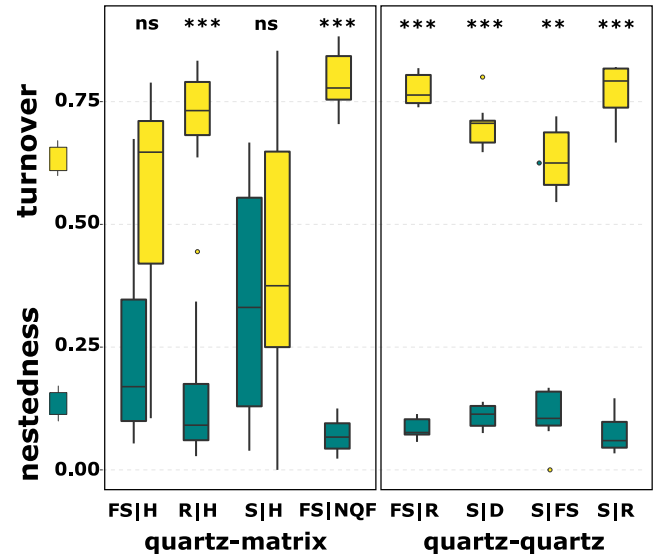


FIGURE 2 Boxplots for all eight boundary types for turnover (yellow color) and nestedness (turquoise color) components. Turnover explained a significantly higher proportion for six boundary types, while for two boundary types ("FS/H" and "S/H"), there was no significant difference between the two components. (FS = *Argyroderma fissum*-*Cephalophyllum spissum*, R = *Ruschia burtoniae*, S = salt pan, D = *Dicrocaulon brevifolium*, H = Heuweltjies, NQF = non-quartz field). Significance levels: ns, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

showed a trend to slightly, but non-significantly increase with increasing differences in soil depth (Figure 3c, Appendix S1).

3.3 | Species composition of habitat types

Non-metric multidimensional scaling of the habitat types (n habitats = 6, n species = 101) indicated differences between groups (three dimensions, stress value = 0.087, Jaccard distance, trymax = 100; Figure 4). The first axis was best explained by the pH value (envfit: $R^2 = 0.47$, $p < 0.001$), while electrical conductivity best explained the second axis (envfit: $R^2 = 0.31$, $p < 0.001$). Soil depth explained low amounts of variation of the first axis (envfit: $R^2 = 0.03$, $p < 0.01$). Soil pH showed a correlation of 0.679 with the first axis and of 0.133 with the second axis, electrical conductivity showed a correlation of -0.150 with the first axis and of 0.535 with the second axis. Subsequent ANOSIM detected significant differences between the six groups (ANOSIM-R = 0.680, $p < 0.001$). ANOVA and Tukey HSD detected significant differences between the scores of several habitat types along the first and second axes (Figure 5, Appendix S2). Along the first and second axes of the NMDS, four main significant groups have formed, respectively (a, b, c, d; Figure 5a). Along the first axis (pH axis), *Dicrocaulon brevifolium* and *Ruschia burtoniae* clustered as acidic quartz habitat types (group a), *Argyroderma fissum*-*Cephalophyllum spissum* and Heuweltjies formed a less acidic group (group b) and the habitat types salt pan (group c) and non-quartz field (group d) formed

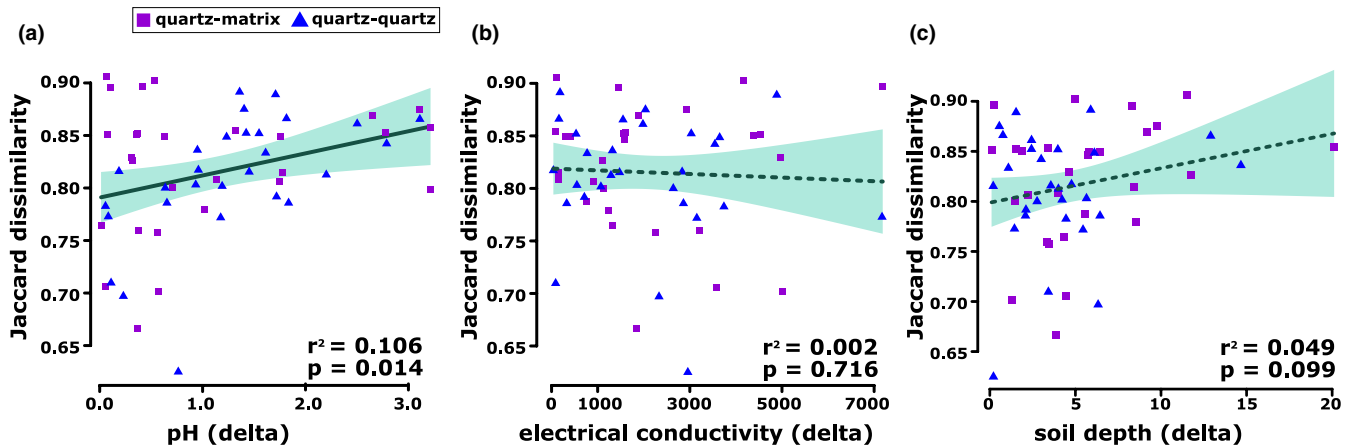


FIGURE 3 Correlation of Jaccard dissimilarity and delta values of adjacent boundary sites ($n = 56$): (a) dissimilarity in species composition significantly increases with increasing differences in pH values between the adjacent transect sites; (b) dissimilarity in species composition does not show any significant change with increasing differences in electrical conductivity; and (c) shows a weak but not significant trend to increase with increasing difference in soil depth

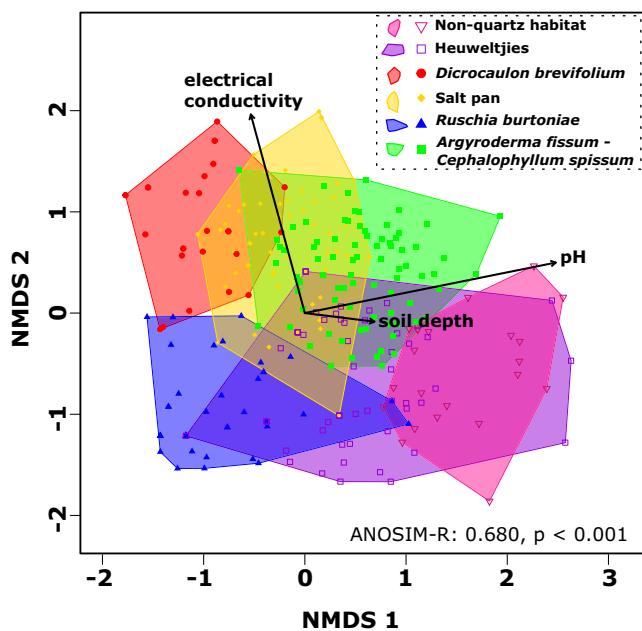


FIGURE 4 Non-metric multidimensional scaling (NMDS) illustrates differences in species compositions of the six habitat types (colored ordihulls). Arrows indicate the three fitted significant environmental parameters electrical conductivity, pH and soil depth. Here, first and second axes are shown, but NMDS was calculated with $k = 3$, based on the Jaccard dissimilarity

independent groups, respectively. Along the second axis (salinity axis), *Dicrocaulon brevifolium* (group a) represents an acidic quartz habitat with increased salinity, salt pan (group ab) and *Argyroderma fissum*–*Cephalophyllum spissum* (group b) represent the saline quartz habitats. *Ruschia burtoniae* formed an independent group (group c), while the two matrix types (Heuweltjies and non-quartz fields) formed a group (group d) with less saline conditions (Figure 5a, Appendix S2). The Kruskal–Wallis test and the Wilcox test detected significant differences in soil pH and electrical conductivity between the

habitat groups. Two groups were formed (a, b) regarding soil pH with *Dicrocaulon brevifolium* and *Ruschia burtoniae* (group a) representing very acidic quartz habitats and all other four habitats (group b) with less acidic soils (Figure 5b). Four groups distinguished according to the electrical conductivity with the salt pan habitats showing the highest salinity values (group a), *Dicrocaulon brevifolium* (ab) and *Argyroderma fissum*–*Cephalophyllum spissum* (group b) with intermediate saline values, *Ruschia burtoniae* and the Heuweltjies (group c) and non-quartz fields (group d) with low salinity values (Figure 5b).

4 | DISCUSSION

All boundary types had high beta diversity (Jaccard dissimilarities) of species composition regardless of which habitat types they bordered on. For six out of eight boundary types, beta diversity was driven by high species turnover between the adjacent habitat types. Our results indicate that species turnover rather than nestedness is the main component of beta diversity in species composition at most boundary types. The intuitive assumption that boundaries between quartz habitats and matrix habitats could be sharper and thus resulting in higher beta diversity cannot be confirmed. On the contrary, the boundaries between quartz habitats show consistently high beta diversity values, which are based on a high species turnover. This indicates that quartz–matrix boundaries are, to a certain degree, permeable for quartz island and matrix species.

4.1 | Species turnover stronger than nestedness component

We confirm our hypothesis that species turnover drives high beta diversity in most investigated boundary types, thus supporting the preliminary indicator species analysis by Schmiedel et al. (2015), which revealed high species fidelity values for most of our habitat types.

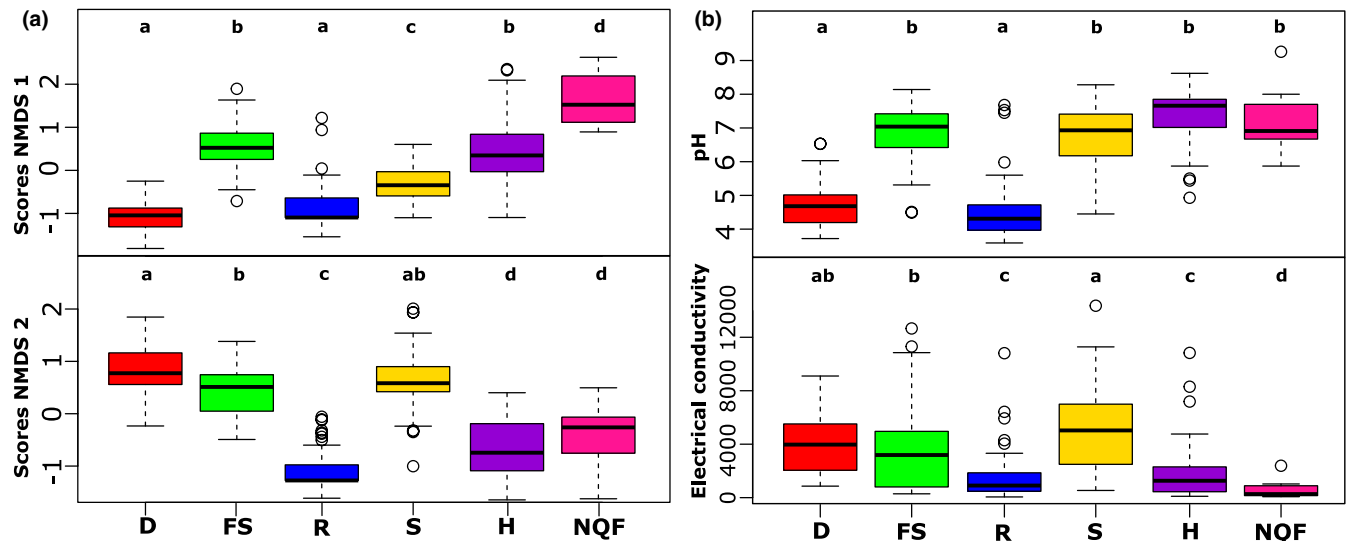


FIGURE 5 (a) Differences between habitat types in the scores along the first and second non-metric multidimensional scaling (NMDS) axis and (b) in soil pH and electrical conductivity (mS/cm). (FS = *Argyroderma fissum*-*Cephalophyllum spissum*, R = *Ruschia burtoniae*, S = salt pan, D = *Dicrocaulon brevifolium*, H = Heuweltjies, NQF = non-quartz field; significant differences between groups are indicated by the letters)

Most species in the study area are habitat specialists, especially species belonging to lineages that evolved in and adapted to the unique but harsh conditions on quartz islands (e.g. 10 out of 11 taxa within the genus *Argyroderma*, which belongs to the ruschioid subfamily of the Aizoaceae are endemic to the Knersvlakte; Schmiedel & Jürgens, 1999; Ellis & Weis, 2006). Species turnover represents the replacement component of beta diversity and indicates that environmental variables control the species assembly of a site (Leprieur et al., 2011). Consequently, it often relates to a higher level of diversification of plant communities, as a higher specialization of species and thus, differentiation of species communities to abiotic site conditions entails a more frequent turnover (Coelho et al., 2018; Fontana et al., 2020). Strong changes in abiotic conditions are usually accompanied by simultaneous biological responses of local species and species communities, resulting in environmental filtering. High species turnover between communities has been shown to be the principal component underlying high beta diversity along strong abiotic gradients for different taxa, e.g. latitudinal (Soininen et al., 2017) or elevational (Coelho et al., 2018) gradients. Topography and climate were suggested to be the main drivers for increasing diversification of plant communities – resulting in high species turnover – with increasing elevation in mountain habitats (Zellweger et al., 2017; Coelho et al., 2018). Our findings are thus in accordance with other studies on partitioned beta diversity along environmental gradients and transition zones. However, the afore-mentioned studies examined partitioned beta diversity at larger spatial scales with climatic or topographic gradients as the main drivers. In contrast, we investigated much smaller-scaled boundaries on the quartz islands of our study area, where microscale soil heterogeneity reflects the spatial distribution of vegetation communities (Schmiedel et al., 2015) and seems to be the principal abiotic factor shaping diversity patterns. Studies investigating the sharp plant species turnover caused by small-scale edaphic gradients are scarce,

presumably because transition types with this grain size seem to occur mainly on sites with special soils in semi-arid or arid environments such as gypsum (Rubio & Escudero, 2000) or serpentine (Harrison et al., 2006); or saline/alkaline soils in grasslands (Cao et al., 2019).

However, for two boundary types, “*Argyroderma fissum*-*Cephalophyllum spissum* to Heuweltjies” and “salt pan to Heuweltjies,” the nestedness of the species composition also contributed substantially to beta diversity and neither of the two components clearly predominated. This is probably due to the comparable species poverty of both habitat types of the boundary type “salt pan to Heuweltjies.” Low alpha diversity of a habitat increases the probability to be merely a subset of the adjacent habitat, provided that at least one species can occur in both habitats. In this boundary type, two species, *Argyroderma crateriforme* (salt pan) and *Drosanthemum pulverulentum* (Heuweltjies), were observed growing across the boundary, which resulted in increased nestedness. Interestingly, both boundary types with higher nestedness values included the matrix habitat Heuweltjies and the respective boundary sites, which had similar soil acidity values. This indicates different possible explanations regarding the transition zones of quartz islands to adjacent matrix habitats. One possibility is the occurrence of so-called ecotonal or edge-related species, i.e. species that only occur in transition zones or close to habitat edges. Ecotonal species, although often suggested to be one among many reasons for increased diversity of ecotones or boundary zones (Odum, 1983), were only found in few empirical studies (e.g. Lloyd et al., 2000; Erdős et al., 2019) and results seem to depend on which definition of ecotonal species was used (Kark, 2013). However, the four species that caused higher nestedness in two of the boundary types by crossing the boundary never occur only in the plots close to the boundary (ecotonal area) but always in the core plots of the habitats as well. In addition, *Argyroderma crateriforme* is a quartz island endemic species (Schmiedel, 2002),

while *Drosanthemum pulverulentum* is typically associated with the Heuweltjies habitat type (Schmiedel, unpublished data). Therefore, we exclude that they represent stable populations of ecotonal or edge-related species and rather consider them to be individuals of species that could establish beyond their habitat range boundaries (discussed as the “mass effect” by Shmida & Wilson, 1985).

This assumption is supported by the fact that several quartz species have been shown in recent germination experiments to be perfectly capable of germinating on soil substrates other than those of their original quartz habitats (Schmiedel et al., 2021). This means that some of the quartz species could grow in matrix habitats, but are outcompeted there probably by biotic interactions (Schmiedel et al., 2021). All tested species, even halophytes and salt-tolerant species, including taxa of the *Argyroderma* genus, needed strong dilution of their original highly saline soils for successful germination (Schmiedel et al., 2021). Thus, seeds of *Argyroderma crateriforme* might also benefit from the less saline conditions at margins of saline habitats or boundary zones (Schmiedel et al., 2015). Soil heterogeneity at these transition zones might be even more fine-scaled than we measured at the 1 m² plot level, which could also be caused by small-scale heterogeneous leaching. On a microscale of a few centimeters, this could lead to a convolution or micromosaic instead of a straight boundary line (Strayer et al., 2003). Mosaicity of vegetation communities across boundaries seems to be a characteristic of other ecotone types (Gosz, 1993; Brownstein et al., 2013), but seems to be highly scale-dependent (Walker et al., 2003). Most of the present plant species are very small (only a few centimeters growth height) and might respond to particularities in soil and topography at microscales (Schmiedel & Jürgens, 1999; Schmiedel & Jürgens, 2004; Ellis & Weis, 2006), which could lead to individual plants establishing in every microhabitat with suitable soil or topographic conditions, no matter how small. Boucher et al. (2017) suggested that this might lead to stronger local adaptations and ecological speciation for individuals of small plant species. Thus, the transition zones of the studied habitats on and between quartz islands do not host unique edge-related species, but species that are at least temporarily able to establish in adjacent habitat types. This might indicate the permeability of the boundary between habitat islands and the surrounding matrix for some species. For some habitat islands, the adjacent matrix could therefore represent rather a source for species than a barrier, which would at least partially question the transferability of island biogeography theory (MacArthur & Wilson, 1967) to habitat islands (Tscharrntke et al., 2012). The insufficiently clarified role of the surrounding matrix type and the challenging question of whether there is a mainland for habitat islands have already been addressed in many studies (Cook et al., 2002; Cook et al., 2004; Kupfer et al., 2006; Itescu, 2018).

Fine-scale partitioning of beta diversity patterns can provide insights how species assemblages are connected with underlying abiotic changes in transition zones, due to the two components representing different processes (Si et al., 2016; Soininen et al., 2017; Fontana et al., 2020). Both deterministic and stochastic processes probably have simultaneous effects on vegetation patterns (Chang et al., 2013; Guo et al., 2018; Mori et al., 2018). However, the predominance of

the species turnover component indicates a preponderance of deterministic processes at the boundary types between the habitats in our study. Deterministic processes, such as environmental filtering, are linked to niche differences of species and imply that abiotic conditions control the species assemblage of a certain site (Levine & HilleRisLambers, 2009; Kraft et al., 2015; Guo et al., 2018). Stochastic processes – such as colonization or extinction, represented by the nestedness component (Clark, 2012; Si et al., 2015; Soininen et al., 2017) – seem to play a similarly important role in the two boundary types discussed in the previous paragraphs, although the low competitiveness of the quartz taxa suggests that this may be temporary.

4.2 | The role of soil environmental parameters for beta diversity

Interestingly, we only found a significant linear increase of the species dissimilarity of the adjacent habitats with increasing dissimilarity in soil pH, while electrical conductivity or soil depth did not show significant linear correlations. This is probably due to two reasons. Firstly, even with minor differences in the soil properties of the two adjacent habitats, all boundary types show a very high beta diversity. Secondly, it must be noted that even a slight increase of the environmental delta value can already mean severe changes; due to the exponential nature of the pH, a difference of 1.0 in delta pH can already mean a transition from e.g. neutral to acidic soil conditions. The soil environmental characteristics of the quartz islands in the study area have already been documented to have strong effects on the taxonomic diversity, the growth form and the local adaptation of plant species (Jürgens, 1986; Schmiedel & Jürgens, 1999; Schmiedel et al., 2015; Ellis & Weis, 2006). While we included quartz–quartz and quartz–matrix boundary types, we did not investigate matrix–matrix boundary types (e.g. Heuweltjies to non-quartz fields), partly because they are not always separated by such distinctive boundaries. Since the zonal matrix habitats usually have less extreme – less acidic, less saline and deeper rootable – soil conditions, including boundary types between them might have changed the pattern of the two non-significant environmental variables.

Soil acidity seems to play a special role in the vegetation composition of some quartz habitats and leads to sharp boundaries with adjacent habitats (Schmiedel et al., 2015). In our study all boundary types including *Ruschia burtoniae* habitats showed a high species turnover and very low nestedness values. High soil acidity can limit plant growth in a number of ways, such as by increasing the mobility of plant-toxic elements or decreasing concentrations of ions that are fundamental for plant growth (Schmiedel et al., 2021). Although we found no significant relationship with increased beta diversity, soil salinity is also an important driver of phytogeography, which is particularly well documented for arid regions and desert ecosystems (Bui, 2013; Ward, 2016). On the quartz islands, soil salinity patterns, in addition to soil pH, influence composition, growth forms, diversification, and probably the high degree of endemism of local plant species (Schmiedel & Jürgens, 1999).

5 | CONCLUSIONS

The small-scaled heterogeneity of soil chemical and physical conditions on quartz islands drives species distribution and composition at the habitat scale and leads to high beta diversity through increased species turnover at the quartz island and landscape (quartz island to matrix) scale. Our results indicate that habitat boundaries within azonal quartz islands and to the surrounding zonal matrix of the Succulent Karoo vegetation contribute to the high regional diversity of this area. Sharp boundaries of small grain size which lead to high beta diversity could thus have an impact on diversity patterns on the landscape scale (gamma diversity), even if local diversity (alpha diversity) is low. Habitat islands represent fragmented systems and naturally come with different boundary types to their adjacent matrix habitats. Partitioning beta diversity along such boundaries can bring valuable understanding about important habitat island–matrix characteristics. Quantifying the proportions of turnover and nestedness enables estimating the sharpness of the environmental and biological contrast to the matrix and thus the matrix permeability potential for certain taxa. Our results indicate that boundaries of habitat islands result in high beta diversity and that matrix habitats might even serve as species pools for some quartz island habitats. As this characteristic is the most fundamental difference to real islands, such studies are an important part of assessing the comparability and applicability of island biogeography theory (MacArthur & Wilson, 1967) to habitat islands.

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AUTHOR CONTRIBUTIONS

US, PE, SI and JO designed the study; AT and NK collected the data under the supervision of US; PE analyzed the data with help of JO; PE wrote the manuscript with contributions of all authors.

DATA AVAILABILITY STATEMENT

Data collected for this manuscript will be made available upon publication in the DRYAD online repository (Eibes, P.M. et al. (2021), Plant diversity across small-scale boundaries, Dryad, Data set, <https://doi.org/10.5061/dryad.4f4qrfjwb>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Linear models colored according to boundary type

Appendix S2. Table with the summary statistics of the non-metric multidimensional scaling (NMDS)

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