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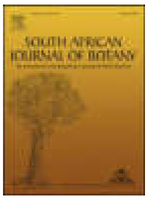

How important is patch size relative to patch isolation in an arid inselberg landscape?

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ABSTRACT

Patch size (area) and isolation (inverse distance to source) are key variables of island biogeography, but their application in conservation planning has recently come under scrutiny. Based on animal distribution data in fragmented landscapes from around the world it was postulated that occupancy was poorly predicted by patch size and isolation. Do these findings also apply to arid areas and to plants?

This question was investigated in four inselberg landscapes in the Namib Desert stretching over a 770 km climatic north–south gradient. Inselbergs (isolated mountains) are special habitats and can be considered 'islands' of more mesic conditions in an arid matrix. Species richness of inselberg specialists was used as an indicator and regressed against area, distance to nearest habitat and distance to 'mainland' (or source pool, which are proxies for level of isolation). Additionally, the influence of landscape geographic position, land use and rock types were studied. Responses of different life forms and individual plant species as well as possible dispersal limitations were also investigated.

Whether patch size is more important than isolation in determining species richness on arid inselbergs could not be answered at a landscape level. However, when investigated on a functional and species level, isolation was of greater importance than patch size for trees and also for selected species such as *Commiphora saxicola* and *Heliotropium steudneri*. The effect of distance to source in this study is likely a function of spatial distance as well as a coast-inland moisture gradient. Inselberg specialist-richness was not affected by land use or the bioclimatic position. Yet rock type, which is a reflection of soil physical and chemical properties did affect species richness with granites and basalts supporting more species. Life forms of inselberg specialists were influenced by the investigated environmental variables, but dispersal limitations were not. Despite inconclusive results at a landscape level, functional groups and individual species provided more conclusive results. This points towards the necessity of additional investigations at a finer scale to gain an understanding of the factors driving species distributions. In future more detail regarding the 'matrix' surrounding 'patches', as well as evolutionary and vegetation historic factors should be explored. Phylogenetic studies would be one tool to help unravelling some of the presently unknown factors affecting species distributions on Namib inselbergs. This study also highlighted the importance of inselbergs in arid landscapes as 'hotspots' of species richness and species of conservation importance.

1. Introduction

Principles of island biogeography such as the importance of area ('patch size' in fragmentation theory) and distance from source (or level of 'isolation') which are widely applied in conservation planning, have been critically reviewed in the last decade (e.g. Loehle, 2007; Laurance, 2008). In a landmark metaanalysis which synthesised animal distribution data (1015 bird mammal, reptile, amphibian and invertebrate population networks) from 89 studies across 6 continents, Prugh et al. (2008) found that patch size and isolation on their own were poor predictors of occupancy for most species. However, patch size and isolation are useful in conjunction with taking account of the properties of the intervening matrix, i.e. type of land cover (Prugh et al., 2008; Franklin and Lindenmayer, 2009). These findings called in question many accepted notions such as the importance of size of patches and connectivity in fragmented landscapes (Goodwin, 2003; Pardini et al., 2010) and ask for critical rethinking in conservation planning. For example, small mammals in a Brazilian Atlantic forest were only affected by patch size at intermediate levels of forest cover. In contrast to areas with low remaining forest cover, where too many native biota were extinct leading to a loss of forest-specialist taxa and thus making patch size irrelevant (Pardini et al., 2010). Prugh and colleagues' extensive study was undertaken for

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animals and included only some studies from arid areas. Evolutionary and ecological processes in arid areas are controlled by different factors than those in more mesic environments (Noy-Meir, 1980) and different responses could therefore be expected. Also the investigated fragmentation in population networks in Prugh et al.'s (2008) study was related to human-induced habitat changes, which are very recent in an evolutionary context and therefore do not incorporate possible adaptations of the affected species or consider historic land use and vegetation history.

On the other hand 'fragmentation' also occurs naturally in landscapes due to differences in environmental factors, resulting in special habitats like wetlands or substrate and topographic 'islands' such as inselbergs (Porembski and Barthlott, 2000). This leads to some general questions: Are the findings with regard to patch size versus isolation in human-induced fragmented landscape valid in ancient, fragmented, natural ecosystems, do these findings apply in arid areas? And do they also apply to plants?

Arid ecosystems, due to their climatic extremes, have often been considered less complex and therefore better suited to study ecological questions that prove difficult in more complex situations (Safriel, 1987). Inselbergs (isolated mountains) in arid landscapes are considered 'islands' because these habitats support a different set of species than the 'zonal' vegetation of lowlands. In arid areas inselbergs support many species with higher moisture requirements, which grow zonal in more mesic bioclimatic zones (Burke, 2004). They can survive on inselbergs in arid zones because inselbergs are cooler, receive more moisture than the surrounding lowlands and provide greater habitat diversity. In tropical areas the opposite applies and inselbergs support more drought-adapted species in comparison to the tropical lowland plants (e.g. Parmentier et al., 2005; Sarthou et al., 2017). Here the lack of soil, organic matter and shade on the rock surfaces leads to greater exposure and run-off and only plants coping with shallow soils and high temperature extremes occupy these inselbergs (Porembski and Barthlott, 2000; Burke, 2003b).

Inselbergs are scattered along the margin of the Namib Desert, which is positioned on the west coast of Africa and stretches over approximately 1000 km. The Namib is characterised by a north–south climatic gradient from subtropical summer to temperate winter-rainfall and a west–east gradient from coastal to more continental conditions inland (Jürgens et al., 1997). Namib inselbergs are of different geological origin from igneous extrusive (basalt) and intrusive (granite) to sedimentary (sandstone) and metamorphic (gneiss) and have been in their current position and configuration at least since the Miocene (Ward and Corbett, 1990). Many plant species growing on these inselbergs are habitat specialists and not found anywhere else and thus endemic (Nordenstam, 1974; Burke, 2002b). Namibia's highest mountain, the Brandberg, is a typical inselberg and harbours seven endemic species which includes herbs, shrubs and dwarf succulents (Craven and Craven, 2000). The reason for their occurrence and thus the factors driving their distribution are still not known (Cowling, 2002). Understanding which factors contribute to the persistence of such specialist plant populations is important for conservation planning and management in arid ecosystems. Testing whether the widely accepted notion of patch size and isolation, two fundamental biogeographic questions, are of relevance contributes to understanding these factors.

The overall questions of this study are: How important is patch size in relation to patch isolation in arid inselberg landscapes in the Namib? How consistent is this across different landscapes and different species? Several sub-questions have been formulated to contribute to answering these overall questions: At a landscape level: Is species richness and diversity affected more by patch size or isolation? What is the effect of other environmental variables such as bioclimatic position of landscape, land use and rock type? To what extent do species traits affect these results? And at a species level, is occupancy of selected inselberg specialists more affected by patch size or isolation?

2. Methods

2.1. Study area

The Namib desert is characterised by aridity (mean annual rainfall below 50–100 mm, Jürgens et al., 1997), a moderate temperature regime near the coast (mean annual minimum and maximum temperature: 10–20 °C), but greater temperature fluctuations inland (mean annual minimum and maximum temperature: 8–36 °C). Fog occurs regularly along the coast and provides additional moisture. Fog's influence decreases along a steep coast-inland gradient of about 50 km (Hachfeld and Jürgens, 2000). Southerly and westerly winds predominate across most of the Namib, disrupted by occasional easterly bergwinds in the southern hemisphere's winter. A weather station near one of the selected inselbergs (Ganab), which is representative of many inselbergs in this study, recorded mean annual rainfall of 129 mm, a mean temperature of 20 °C and mean minimum and maximum temperature of 7 and 31 °C (Berger et al., 2010).

Four inselberg landscapes were investigated. These were from north to south: the Etendeka-Barab (ETE) (geographic centre: 19°45′S and 13°50′E), Spitzkoppe–Twyfelfontein (STL) (geographic centre: 21°08′S and 14°33′E), Ganab (GAN) (geographic centre: 23°11′S and 15°29′E) and Namibrand (NRL) inselberg landscape (geographic centre: 25°14′S and 15°51′E), situated along a 770 km north–south climatic gradient (Fig. 1). The Etendeka-Barab inselberg landscape encompasses flat-topped table mountains of volcanic origin in the northern Namib, stretching from the Grootberg massif to inselbergs along the Barab River in the west. The inselbergs are of Triassic to Jurassic age of the late Karoo period in Namibia and were formed from basalt and related extrusive lava during the break-up of Gondwana (Erlank, 1985; Miller, 2008). The Spitzkoppe–Twyfelfontein inselberg landscape is positioned in the central Namib at a break of the escarpment. These inselbergs are of Cretaceous age (Miller, 2008). The Spitzkoppe–Twyfelfontein landscape includes the Brandberg, which is the highest mountain in Namibia, granite inselbergs to the northeast of the Brandberg and the granite and dolerite inselbergs around Spitzkoppe. The Ganab inselberg landscape encompasses three granite inselbergs in the southern part of the central Namib, north of the northern boundary of the Namib sand-sea. These are older than the Spitzkoppe inselbergs and originate from the Damara orogen period at about 800–600 million years ago (Miller, 2008). The Namibrand inselberg landscape in the southern Namib stretches from the Namib sand sea to the Nubib Mountains which form part of the Western Great Escarpment in southern Africa. These

Fig. 1. The position of the four study areas in Africa and Namibia.

inselbergs are of Precambrian age of the Sinclair formation (Miller, 2008) and are composed of gneiss–granite rock types. The inselbergs are scattered to the west of the Nubib Mountains and the escarpment. Shallow regosols, largely determined by the underlying rock types (Burke, 2002a) characterise the soils on all inselbergs.

All inselberg landscapes are positioned in areas zoned for conservation, either protected as a private nature reserve (Namibrand), in a state-protected area (Ganab) or communal conservancies (Etendeka–Barab and Spitzkoppe–Twyfelfontein landscape). Yet these landscapes do not receive the same level of protection. Livestock farming is practiced in the conservancies, and quarrying and small-scale mining for gemstones takes place in the Spitzkoppe area. All 'mainland' areas are in commercial farmland, except for the northern-most landscape, which is in communal conservancies.

The Supplementary material (Annex Table 1, Appendix 1, 2 and 3) illustrates the characteristics of the study areas, survey methodology and selected plant species, and includes a species list of inselberg specialists and their attributes from this study (Annex Table 2).

2.2. Nature of the dataset

Floristic data were compiled from the authors' database of inselberg floras in Namibia which were collected over a period of 17 years (1998–2015). Information on data collection protocols is included in Supplementary material (Appendix 3). Due to variability and patchiness of rainfall in an arid environment recording was undertaken over many years (Burke et al., 1998; Burke, 2002b, 2003a). Recording and collecting of plant species took place when a good to exceptionally good rainy season at an inselberg provided the most complete inventory. The scale of analysis for this study was regional or gamma diversity (McCain and Grytnes, 2010), which consisted of a plant species list for the entire inselberg. Species lists were compiled for each inselberg by aggregating more detailed data and averaging abundances where necessary. A minimum value of 0.1 cover was applied to each taxon. In order to minimise the 'noise' in the data caused by widespread, generalist plant species (Cook et al., 2002), the analyses focussed on inselberg specialists. These were defined as all species present on inselbergs, but not present in the surrounding lowland landscape. This included species which were not recorded in the inselberg landscape under investigation in surrounding lowlands, but could occur in lowland habitats elsewhere (e.g. *Cryptolepis decidua*). There are no exotic inselberg specialists.

2.3. Data analysis

2.3.1. What are the compositional differences between the inselberg floras?

Non-metric multi-dimensional scaling (NMDS) with Bray–Curtis similarity as a distance measure was applied using the computer programme PAST (Hammer et al., 2001). NMDS is a non-parametric ordination and thus suited for not normally distributed data. Two-dimensional and 3-dimensional models were run, and the data were tested overall as well as individually per inselberg landscape. Data from different landscapes were also combined to test for the effect of geographic position. A hierarchical, unconstrained cluster analysis, based on a Bray–Curtis similarity matrix and illustrated using paired groups, was employed to further elucidate the NMDS results (Hammer et al., 2001).

2.3.2. Is species richness and diversity affected more by patch size or isolation?

Patch size was defined as the base area of an inselberg, which had shown to be a reasonable approximation of surface area in a previous study (Burke et al., 2003). For ease of reference, surface or base area will be referred to as 'area' in this study. In biogeographical term 'isolation' is expressed as a function of the nearest distance to a mainland area and to the closest similar habitat patch (Prugh et al., 2008). In this study distance to 'mainland' was measured as the nearest distance between the margin of the inselberg/mountain and margin of the escarpment or highland area. The Erongo mountains and the Brandberg were defined as 'mainlands' in the STL, but the edge of the Great Western Escarpment formed the 'mainland' for all other inselbergs not in the vicinity of the Brandberg or Erongo Mountains.

In addition to species richness (number of taxa), the Shannon diversity index and Simpson index were calculated with the computer programme PAST (Hammer et al., 2001). The Shannon index (Pielou, 1969) combines species numbers and abundances and is calculated as follows:

$$\text{Diversity } H' = -{}^{s}\Sigma_{i} n_{i}/n * \ln n_{i}/n$$

Where by s = number of species, n = total abundance, n_i = proportion of abundance of taxon i, ln = log base $_n$.

The Simpson index 1 − D measures 'eveness' (Harper, 1999) and is calculated as follows:

$$\text{Simpson index } 1 - D = 1 - \Sigma_{i}(n_{i}/n)^{2}$$

Where by n = total abundance, n_i = proportion of abundance of taxon i,

All variables were tested for normality. Distance to nearest habitat, height above surrounding and area were not normally distributed and required log-transformation. One outlier was also removed from the dataset. The resulting dataset consisted of 35 sites, 493 species of inselberg specialists and a total of 1569 records. Multivariate linear regressions with one independent variable (species richness, Shannon diversity or Simpson index) and three dependent variables (log-transformed area, distance to mainland and log-transformed nearest habitat) were performed using the computer programme PAST (Hammer et al., 2001). A significance level of 5% was used.

2.3.3. Could other environmental variables influence these results?

In order to control for size of individual inselbergs, species richness per height above surrounding was calculated per inselberg and compared between landscapes, land use and rock types (species richness per km^2 was highly skewed by small inselbergs and therefore height above surrounding was used to control for size). The rock types basalt, dolerite, granite and gneiss were encountered. Kruskall Wallis Analyses of Variance (ANOVA), followed by Mann–Whitney pair-wise comparisons (Zar, 1996) were employed and a significance level of 5% was used in all statistical analyses.

2.3.4. What is the effect of species traits and possible dispersal limitations?

Life forms were assigned for each inselberg specialist according to standard definitions (Ellenberg and Mueller-Dombios, 1967; Germishuizen and Meyer, 2003). This resulted in the following categories for plant species in this study: tree, tall stem-succulent, shrub, herb, grass, fern, geophyte, herbaceous perennial and leaf-succulent. Dwarf stem-succulents (< 30 cm height) were included in leaf-succulents because tall stem-succulents follow a life strategy more resembling that of trees, while dwarf stem-succulents are more similar to leaf-succulents in their life history strategy (von Willert et al., 1990).

Dispersal strategy was classified according to adaptations for seed dispersal and grouped as long-range and short-range. Self- (ballistic) dispersal, dispersal by water or where no specific adaptation for seed dispersal was evident were all classified as short-range dispersal, as diaspores hardly reach dispersal distances over 300 m (Cain et al., 1998). Adaptations for animal and wind-dispersal were classified as long-range dispersal. In the context of this biogeographic study the dispersal syndromes were combined to long- and short-range dispersal as potential dispersal distance rather than the dispersal vectors are of importance to contribute to answering the posed questions. The life form categories shrubs and leaf-succulents were not normally distributed and log (x + 1) transformed (Fowler and Cohen, 1992). The number of species with a particular life form or dispersal range per inselberg was regressed against three dependent variables (log-transformed area, distance to mainland and log-transformed nearest habitat).

Whatever general patterns may emerge, they present a cumulative response from individual species. Understanding responses at a species level will provide another level of depth to the question of relative importance of patch size versus isolation. This was therefore also investigated at a species level for selected inselbergs specialists. In order to obtain statistically meaningful results, only inselberg specialists which occurred at 10 or more sites, which is on nearly one third of the inselbergs, were included. Point-biserial correlation coefficients (non-parametric) between occupancy, patch size (area) and isolation (distance to mainland and nearest habitat) were calculated for presence/absence data. The following formula was used:

$$r_p = |M_p - M_q|/S_x * \sqrt{(p * q)},$$

where r_p = point-biserial correlation coefficient; M_p = mean of the first group of values, M_q = mean of the second group of values; p = proportion of observations in the first group; q = proportion of observations in the second group; and S_x = standard deviation of all observations on the continuous variable (Kent and Coker, 1992).

3. Results

The 493 inselberg specialists included in this analysis presented a wide array of adaptations in life forms and dispersal strategies. This also included a number of species endemic to Namibian inselberg and mountain habitats. The succulents *Adromischus schuldtianus, Aloe sladeniana, Cyphostemma bainesii, Hoodia ruschiii* and *Othonna brandbergensis* and the shrubs *Eriocephalus pinnatus, Hermannia merxmuelleri, Marcelliopis splendens, Plumbago pearsonii* and *Tephrosia griseola* were found to be restricted to inselberg and mountain habitats in Namibia. No plant species included in this study were restricted to one particular inselberg or mountain. Also a number of red-listed plants occurred on inselbergs such as *Aloidendron dichotomum, Cyphostemma ruacanense, Eberlanzia sedoides, Eriocephalus kingesii, Lithops schwantesii, Lessertia acanthorachis* and *Pegolettia plumosa.*

3.1. Compositional patterns of the Namib inselberg floras

The non-metric multidimensional scaling produced very high stress values for all data combined, as well as for the individual inselberg landscapes, except for the Etendeka–Barab landscape (Table 1). Stress values over 0.3 are generally considered difficult to interpret as the ordination presents an arbitrary rather than species relationship-related placing of points in multi-dimensional space (Clarke and Warwick, 1994). The NMDS results (Fig. 2) were only to some extent corroborated by the cluster analysis (Fig. 3). Only the close groupings of Heinrichsberg (HEIN), Amichab (AMI) and Gross Spitzkoppe (GR_SPK) in the Ganab and Spitzkoppe–Twyfelfontein landscape and the distinctiveness of Klein Spitzkoppe (KL_SPK) were also clearly indicated in 2-dimensional space in the NMDS ordination (Fig. 2). None of the other clusters in the dendrogram (Fig. 3) were reflected in the NMDS. Combined with the high stress value, the NMDS can thus not be interpreted further in more detail.

Table 1
Results of the non-metric multi-dimensional scaling (bold = interpretable ordination).

Data	Stress 2D	Stress 3D
All inselbergs	0.685	0.660
Etendeka-Barab landscape	**0.184**	**0.148**
Spitzkoppe–Twyfelfontein and Ganab landscaoe	0.4	0.489
Spitzkoppe–Twyfelfontein landscape	0.446	0.429
Spitzkoppe–Twyfelfontein landscape without northern inselbergs	0.444	0.442
Namibrand landscape	0.628	0.598

The exception was the Etendeka–Barab landscape where NMDS of the eight inselbergs showed a cluster of three floristically related inselbergs (N-Barb, 25 and Gomakukous), while all other five inselbergs were positioned in a circle almost equally far apart from the central cluster and each other (Fig. 4).

The cluster analysis on the other hand provided a more interpretable reflection of floristic relationships between these inselbergs and indicated that spatial position is important in some instances. For example some inselbergs in close proximity to each other also showed a high overlap in floristic composition (e.g. Chowagas-SW, HaiberF-kop1 and HaiberF-kop3, BL_RAN and SS_SPK as well as BLAA1 and BLAA3). The latter are very close (1.3 km apart), while inselbergs of the other two groupings are no more than 30 km apart. But not all floristically close inselbergs in the cluster analysis were also spatially close. Gomakukous and GRK1 are 143 km apart and Klipkop and Tumasberg are separated by 183 km. No groupings clearly according to rock type or land use were observed.

3.2. The effect of patch size and isolation on species richness and diversity

The definition of patch size as the base area of an inselberg was confirmed as a reasonable approximation of surface area by a moderately strong, significant correlation ($r^2 = 0.48$, $p > .001$) between base area and height above surrounding.

Species richness ranged overall 3–108 species per inselberg, with the greatest range in the Namibrand landscape (5–108 species). Likewise the greatest range in Shannon diversity (1.61–4.22) and Simpson index (0.25–0.97) was found in the Namibrand landscape. Species richness of inselberg specialists was poorly explained by the environmental variables area, distance to mainland and distance to nearest habitat (Figs. 5, 6 and 7). The model only returned a weak correlation overall ($r^2 = 0.06$), although statistically significant. The correlation coefficient for log-transformed area was highest, showing a weak correlation ($r^2 = 0.16$) of low significance (Table 2). Both measures of species diversity (Shannon and Simpson) returned an overall very weak model which was not significant. Very weak and non-significant correlations of the species diversity indices with the investigated variables warrant no further interpretation or analysis of the diversity measures (Table 2).

3.3. The effect of position of landscape, land use and rock type

Analysis of variance showed that there were no significant difference between the four landscapes in species richness of inselberg specialists (Kruskall Wallis H = 1.8, p = .61), nor in land use (Kruskall Wallis H = 2.8, p = .1).

With regard to rock types, there was a significant difference (Kruskall Wallis H = 8.84, p = .03) with the extrusive rocks basalt and dolerite clearly set apart from the granite and gneiss when tested in pairwise Mann–Whitney U-tests. The basalts in the Etendeka–Barab landscape and the granites in the three other landscapes supported the highest species richness (mean: 0.21 species/m height for basalt and 0.26 for granite), while dolerite supported substantially lower species richness (mean: 0.08 species/m height).

3.4. The effect of species traits

3.4.1. Life form

Five regression models of the nine types of life forms showed overall significant correlations between the type of life form and the environmental variables area, distance to mainland and to nearest habitat, namely shrubs, geophytes, herbaceous perennials, trees and leaf-succulents (Table 3 section A). The correlation was very weak for shrubs, geophytes, herbaceous perennials and leaf-succulents, but moderate for trees ($r^2 = 0.32$) (Fig. 8). A negative, significant correlation to distance to mainland indicated that this was the most important variable for trees. Area indicated a positive, significant

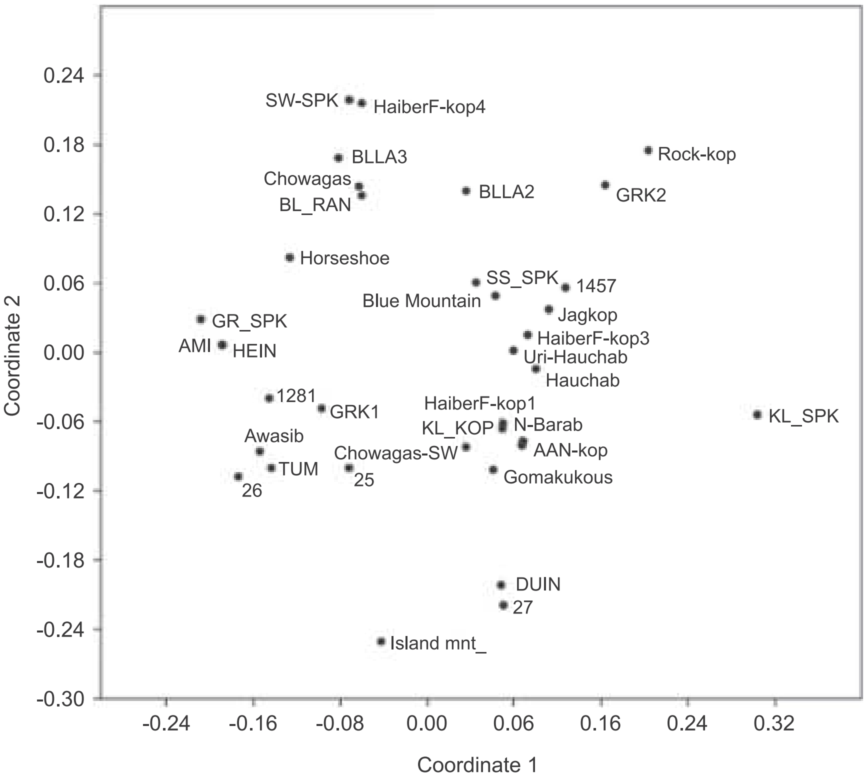

Fig. 2. Non-metric multi-dimensional scaling (NMDS) of all inselbergs.

correlation for geophytes and leaf-succulents. There were also significant correlations between herbaceous perennials and stem-succulents with area, between grasses and distance to mainland, and trees with distance to nearest habitat. But these correlations were weak ($r^2 < 0.2$). The correlations were sufficiently different between the nine life forms to expect a different response to the environmental variables for each life form group (Table 3 section A).

3.4.2. *Dispersal limitation*

Although both regression models dealing with dispersal were overall significant, they were very weak (Table 3 section B). It is interesting to note that adaptations for short- or long-range dispersal were almost evenly distributed amongst inselberg specialists. Considering individual environmental variables, only area showed a significant, but weak correlation ($r^2 = 0.11$ and 0.18 respectively) with species adapted for long-range dispersal and for short-range dispersal. Unlike for life forms, where correlations for the life form groups differed, the dispersal categories assigned in this study produced similar correlations for long- and short-range dispersal in the regression models. Patterns in correlation coefficients overall and with the three environmental variables as well as significance were maintained for the long- and short-range dispersal regressions (Table 3 section B).

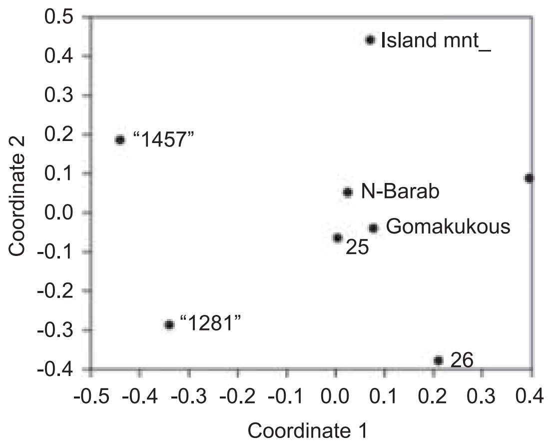

Fig. 3. Non-metric multi-dimensional scaling of the inselbergs in the Etendeka-Barab landscape.

3.5. *Are there differences between species?*

Only few inselberg specialists occurred sufficiently frequent to warrant a statistical analysis testing occupancy in relation to the three environmental variables area, distance to mainland and to nearest habitat. Although the species level investigation was thus for practical reasons limited, 15 inselberg specialists were frequent across all inselbergs. They included shrubs, trees, herbs and one stem-succulent. Approximately half of these showed adaptations for short-range dispersal, half for long-range dispersal. Distance to mainland was the environmental variable most frequently indicating a significant, modest correlation and this was the case for *Abutilon pycnodon, Barleria rigida, Commiphora saxicola, Helichrysum tomentosulum, Heliotropium steudneri* and *Sterculia africana* (Table 4). The shrub *Barleria rigida* also showed a significant correlation with area, as did *Berkheya spinosissima*. *Limeum aethiopicum* showed a significant correlation with distance to nearest habitat. All these have short dispersal ranges, except for *Commiphora saxicola*, which is animal-dispersed and *Berkheya spinosissima* and *Helichrysum tomentosulum* which are wind-dispersed. The latter three could therefore reach longer dispersal distances.

4. Discussion

Recent studies have questioned the application of key variables of island biogeography, patch size (area) and isolation (inverse to

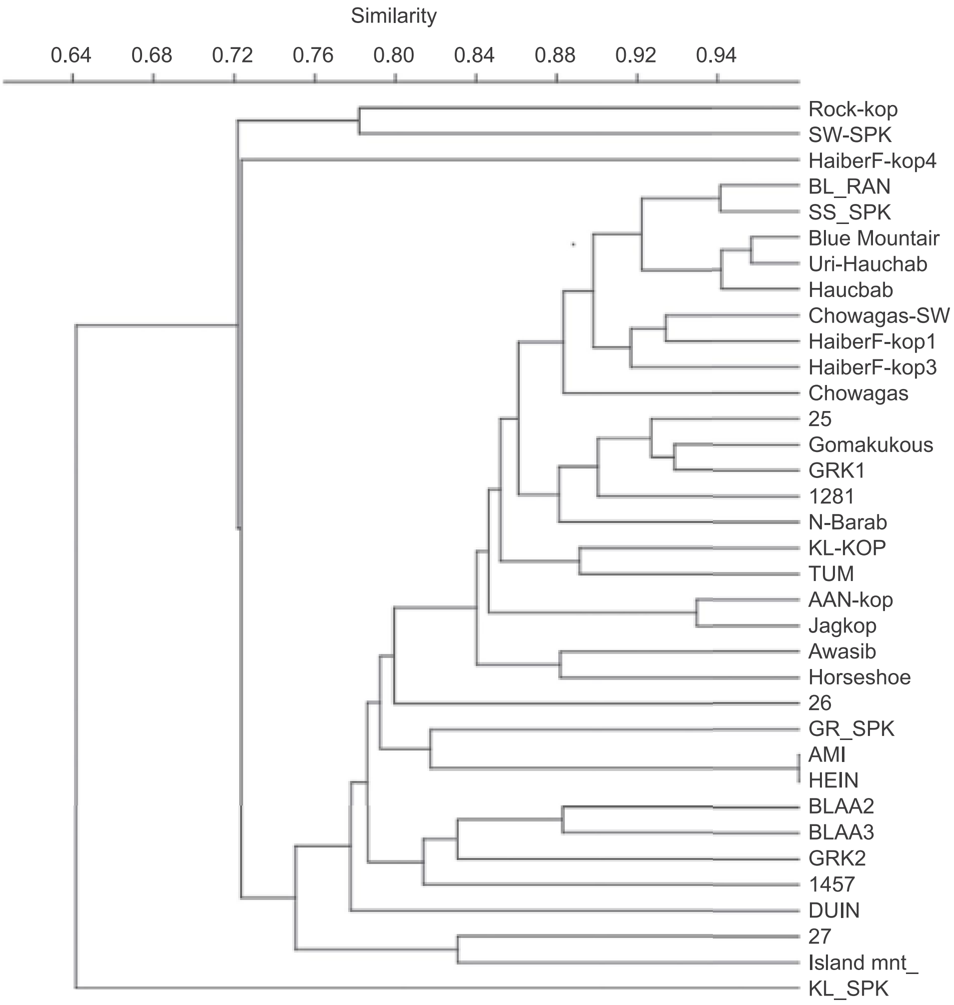

Fig. 4. Dendrogram of cluster analysis with Bray–Curtis similarity values of all inselbergs.

distance to source) in conservation planning (Laurance, 2008; Franklin and Lindenmayer, 2009). Their relevance in different environmental settings and for different groups of taxa therefore needs to be better understood. This study investigated an arid setting, using plant species as indicators. The relative importance of patch size versus isolation at a landscape level could not be clearly established, but a different response by various life forms and individual species was evident.

4.1. Floristic relationships between inselbergs

Describing species compositional patterns provided an additional variable for interpreting species richness and diversity patterns in relation to patch size and isolation. The unfolding picture is complex, but supports the notion that multiple environmental variables (e.g. biogeographic position, reflecting current and past climate, as well as spatial situation, underlying substrate, height and area of inselberg)

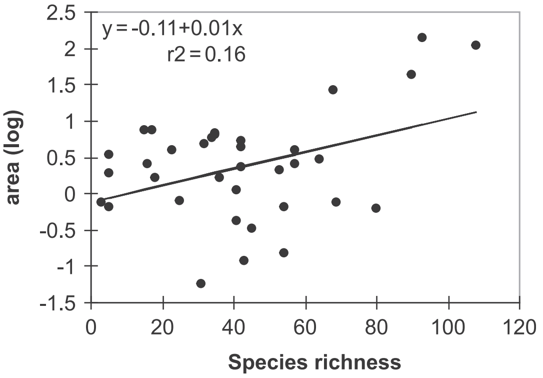

Fig. 5. Regression of species richness of inselberg specialists and area (log-transformed) in four Namib desert inselberg landscapes (n = 35).

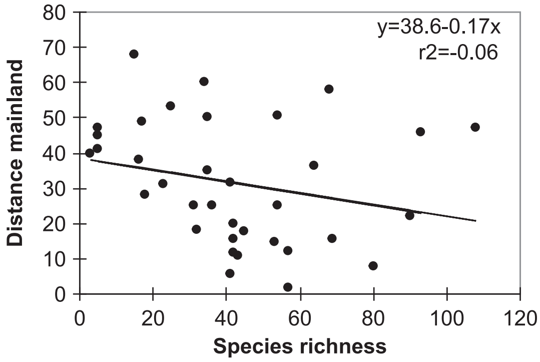

Fig. 6. Regression of species richness of inselberg specialists and distance to mainland in four Namib desert inselberg landscapes (n = 35).

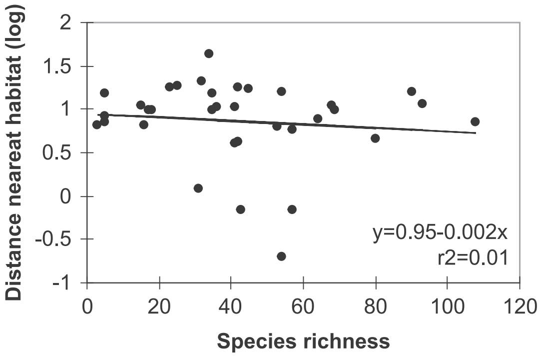

Fig. 7. Regression of species richness of inselberg specialists and distance to nearest habitat in four Namib desert inselberg landscapes (n = 35).

act in concert. The patterns derived from ordination and cluster analyses only coincided in two instances: (1) the Klein Spitzkoppe inselberg is floristically quite distinct and (2) one group of large inselbergs in the central Namib (Heinrichsberg, Amichab and Gross Spitzkoppe) are floristically close, although the distance between Heinrichsberg and Gross Spitzkoppe is 156 km. Klein Spitzkoppe is the second highest granite inselberg in the Spitzkoppe–Twyfelfontein landscape and shaped in a way which provides a larger surface area in its upper reaches than the other high granite inselbergs in this landscape. It harbours the highland and escarpment shrub *Aspilia eenii* in abundance and the sedge *Bulbostylis hispidula* which were not recorded on any other inselberg. The grouping of Gross Spitzkoppe, Amichab and Heinrichsberg is more difficult to explain, as these only share species which also occur on other inselbergs, such as *Amphiasma divaricatum, Berkheya spinosissima, Dauresia alliariifolia, Enneapogon scaber* and the resurrection bush *Myrothamnus flabellifolius*, but none of the less frequently recorded species. The complexity is reflected by groups of inselbergs which are spatially and floristically close such as medium-sized inselbergs in the Haiber flats area of the Namibrand inselberg landscape (HaiberF-kop1 and 3 and Chowagas-SW), medium-sized dolerite ridges (BL_RAN and SS_SPK) and two granite outcrops (BLAA1 and BLAA3) in the Spitzkoppe–Twyfelfontein landscape. This is contrasted by floristically close inselbergs which are over 140 km apart, and are positioned in different inselberg landscapes (Gomakukous – GRK1 and Klipkop – Tumasberg, and the group mentioned above). Here either environmental factors other than biogeographic and spatial position come into play, or the ordination does not illustrate the floristic relationships realistically.

In the more homogenous Etendeka–Barab landscape (all inselbergs are flat-topped basalt mountains) the ordination can be interpreted as showing three floristically close inselbergs (Fig. 3). Commonalities here are that the spatial distance between these ranges 16–33 km and they are medium-sized (170–222 m height above surrounding and 0.15–1.7 km^2 area). The floristically less similar inselbergs are either very high, closest from the mainland area or cannot be characterised by the investigated environmental factors.

Table 2
Summary of results of multivariate linear regression of inselberg specialist species richness, Shannon diversity index and Simpson index on area (log-transformed), distance to mainland and distance to nearest occupied habitat (log-transformed).

	r^2	p	r^2	p	r^2	p
	Species richness		Shannon		Simpson	
Overall statistics	0.06	0.004	0.002	0.44	0.002	0.92
Dependent variables	**r^2**	**p**	**r^2**	**p**	**r^2**	**p**
Area (log)	0.16	0.017	0.06	0.15	0.003	0.75
Distance to mainland	−0.06	0.150	0.002	0.8	0.002	0.82
Distance to nearest habitat (log)	−0.01	0.504	0.002	0.8	0.005	0.70

Table 3
Results of multivariate linear regression on different life forms and dispersal range of inselberg specialists with area (log-transformed), distance to mainland and distance to nearest habitat (log-transformed) (* = significant at a 5% level, bold = correlations which warrant consideration).

	Overall statistics r^2	Area (log) r^2	Distance to mainland r^2	Distance to nearest habitat (log) r^2
(A) Life form				
Shrubs (log (x + 1)) (n = 204)	0.08*	0.08	−0.08	−0.02
Herbs (n = 111)	0.05	0.05	−0.05	−0.01
Grasses (n = 50)	0.15	0.02	−0.15*	−0.03
Geophytes (n = 25)	0.019*	**0.38***	0.018	0.013
Herbaceous perennials (n = 18)	0.017*	0.16*	−0.017	0.002
Trees (n = 33)	**0.32***	−0.15	−**0.32***	−0.15*
Leaf-succulents (log (x + 1)) (n = 27)	0.01*	**0.34***	0.01	0.01
Stem-succulents (n = 23)	0.001	0.15*	0.001	0.03
Ferns (n = 4)	0.07	0.02	−0.07	−0.09
(B) Dispersal range				
Short-range (n = 247)	0.08*	0.11*	−0.08	−0.01
Long-range (n = 248)	0.05*	0.18*	−0.05	−0.02

4.2. *The effect of patch size and isolation on species richness and diversity*

On a landscape level, neither patch size nor isolation showed convincingly strong correlations with species richness of arid inselberg specialists (Table 2, Figs. 5, 6 and 7). Although area showed the strongest correlation amongst the environmental variables, the correlation was weak and barely significant (Table 2). So this cannot be regarded as a clear indication that area is more important than isolation. The diversity measures showed no correlation at all with the investigated variables (Table 2). This may point (1) towards variability in the data or (2) to other factors influencing species richness and diversity of inselberg specialists which were not investigated in this study. Additional environmental variables, possibly operating at different scales (Bestelmeyer et al., 2006), are likely important. These could include other niche factors (Auerbach and Shmida, 1987) (e.g herbivory), affected by local climatic conditions (Gurvich et al., 2014) as well as spatial aspects (e.g. nature of the surrounding lowlands). Considerable variability in response data have also been the cause of poor correlations between species richness and investigated habitat parameters in similar studies (e.g. Lindenmayer et al., 2005). Most likely a combination of the investigated variables and some not

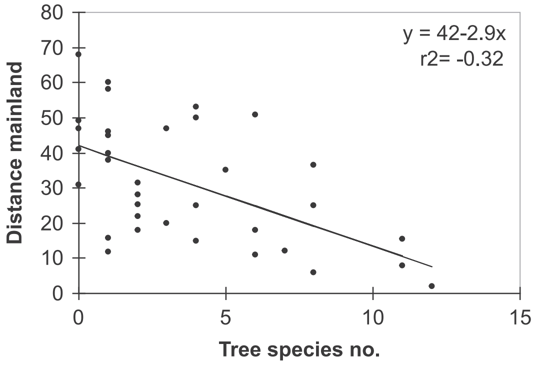

Fig. 8. Tree species richness and distance to mainland in Namib desert inselberg landscapes (n = 35).

Table 4
Point-biserial correlation coefficients between selected inselberg specialists and the environmental variables area, distance to mainland and distance to nearest habitat (* = significant; – = insufficient data; bold = significant correlations).

Plant species	n	Area	Distance to mainland	Distance to nearest habitat
Abutilon pycnodon	13	0.33	**0.48***	0.30
Barleria rigida	12	**0.38***	**0.39***	0.15
Berkheya spinosa	10	**0.43***	0.07	0.04
Commicarpus squarrosus	16	0.02	0.06	0.12
Commiphora saxicola	11	0.23	**0.37***	0.25
Dauresia alliarifolia	12	0.22	0.20	0.21
Euphorbia guerichiana	11	0.21	0.02	0.09
Forsskaolea candida	10	0.14	0.24	0.18
Helichrysum tomentosulum	24	0.15	**0.41***	0.28
Heliotropium steudneri	10	0.22	**0.36***	0.31
Limeum aethiopicum	10	0.09	0.17	**0.35***
Polygala guerichiana	18	0.15	0.23	0.22
Sericocoma heterochiton	10	0.10	0.22	0.19
Solanum rigenscentoides	12	0.26	0.23	0.20
Sterculia africana	12	0.25	**0.61***	–

included in this study act in concert in controlling species richness and diversity at a landscape level (Zobel, 1997).

In contrast to various studies in tropical mountain regions (Kessler, 2002; Jacquemyn et al., 2007; Sklenář et al., 2013) well as globally (Porembski et al., 2000; McCain and Grytnes, 2010), this study revealed no significant effect of area. In the cited studies elevation and area were reported to have a great influence on species richness overall. This could well be related to the different scale of these studies in which regional parameters override the influence of landscape level and local effects (Taplin and Lovett, 2003). Where greater elevational gradients were investigated (e.g. Kessler, 2002) larger habitat diversity and climatic altitude gradients would be encountered, thus accounting for a greater effect of area. In tropical alpine floras of South America and New Guinea, for example species richness was well correlated with log-transformed area (Sklenář et al., 2013). On a landscape level, a study of cacti communities in semi-arid southern Brazil found a positive correlation with area, while negative with the distance to nearest outcrop (Saraiva and Souza, 2012), indicating (1) that both patch size and isolation were important, and (2) that patterns are more likely detected when groups of plants with similar functional properties are investigated.

4.3. The effect of landscape, land use and rock type

When controlled for size of inselberg, there were no significant differences in inselberg specialist richness between the landscapes, which represent geographic position, and with this climate as well as spatial configuration. Ordinations of floristic composition did not provide clear indications of distinct groupings which could be associated with obvious environmental or spatial variables and therefore did not contribute further insights to this study. Although the landscapes are aligned along a 770 km north–south gradient, similar climatic conditions (they all fall into the desert and transition to savanna and Nama Karoo biomes on the escarpment) probably resulted in a saturated species pool for this type of habitat and bioclimatic zone (Caley and Schluter, 1997). There are differences in local climate but these are not affecting species richness overall. For example the northern-most inselbergs receive no rains in winter, while rains occasionally fall in winter on the southern-most inselbergs. Species richness of inselberg specialists was also not significantly influenced by land use. Although land use is conservation-orientated in all study sites, there are differences. Livestock-farming is not practised in state-protected areas, while this is the case in conservancies. Yet rocky habitats are generally better buffered against grazing impacts (Hoffman and Rhode, 2010), as livestock mostly grazes and browses in lowlands. Inselbergs are therefore less likely to be affected by grazing pressure.

Rock types, on the other hand, reflecting soil chemical and physical properties, resulted in differences in species richness of inselberg specialists, with the dolerite ridges in the Spitzkoppe–Twyfelfontein landscape clearly less species-rich than the granite and gneiss inselbergs and the basalt table-top inselbergs. The importance of rock type in structuring plant communities of inselberg landscapes in the Namib had been detected previously, when a range of inselbergs with different substrates was investigated (Burke, 2001). Soils derived from basalt and dolerite are more fertile than those derived from granite and gneiss (Burke, 2002a), but the dolerite inselbergs supported the lowest species richness. Rock type not only determines the chemical properties of the substrate (Burke, 2002a; Williamson and Balkwill, 2013), but also physical parameters such as water-holding capacity and stability. This is supported by findings from a study in the tropical Andes where species richness of mountain summit vegetation clearly declined on scree, which is likely related to the lack of stability of this substrate (Cuesta et al., 2017). The dolerite ridges in this study present the least stable substrate, as the slopes are steep and the upper sections are covered in loose rock fragments. Although the upper slopes of the table-top inselbergs in the Etendeka–Barab landscape are also steep, the basalt formation provides a more stable substrate. Rock type also proved important in structuring inselberg plant communities in Madagascar with differences clearly evident between limestone, granite and sandstone inselbergs (Fischer and Theisen, 2000).

4.4. The effect of species traits

To what extent do species traits influence these results? The life forms were influenced differently by the investigated environmental variables (Table 3 section A), indicating that life forms had an effect on the relative importance of area and isolation on species distributions in the study area. However, only one correlation was adequate to show a direct link to one of the investigated environmental variables: the number of trees was significantly, negatively, though weakly correlated with distance to mainland. This means that the distance to the source pool does contribute to explaining occupancy of a particular inselberg in this instance. Tree species numbers decrease on inselbergs with increasing distance from mainland (i.e. source). This was not the case for any other life form, although significant, but weak, positive correlations were indicated for geophytes, herbaceous perennials and leaf-succulents with area. The overall regression models were, however, weak ($r^2 < 0.02$), thereby reducing the strength of the correlations. The moderate correlations between geophytes and leaf-succulents and area still warrant consideration though. While field data related to geophytes are possibly under-represented (once-off surveys as employed in this study may not capture all early emerging plants such as geophytes), the leaf-succulents are likely not poorly recorded. This indicates that there is possibly an increase of succulent species with the size of inselbergs. This may be a reflection of microclimatic conditions which improve for succulents with higher elevation. Cooler and more moist conditions are associated with many mountain tops in arid regions and this could well explain the increasing species richness of succulents. A study of Namib inselbergs along elevation gradients corroborated this pattern clearly for central Namib inselbergs, but not for the Etendeka inselberg landscape (Burke, 2013).

In this study the distance from source is not only a spatial function, but also presents a climatic gradient of decreasing rainfall with increasing distance from source. With one exception (some inselbergs in the Spitzkoppe–Twyfefelfontein landscape which are in the vicinity of the Brandberg), all 'mainland' areas are the escarpment which is to the east of the inselbergs and in a higher rainfall regime. There is a coast-inland gradient of increasing rainfall in the Namib (Jürgens et al., 1997), thus inselbergs closer to the escarpment are not only closer to a source pool, but also receive higher rainfall. To some degree this also applies to inselbergs around the Brandberg massif, as this mountain complex is sufficiently large to generate its own climate (Breunig, 1990) and may therefore also affect inselbergs in its vicinity. The trees' response to a large-scale geographic parameter (distance to source) could thus also point to trees having a lower fitness in marginal habitats (Grime, 1979) which receive lower precipitation. All other life forms in this study are likely governed by a combination of variables operating at local scales. Altitude as such, for example played an important role on cacti life form richness in Argentina (Gurvich et al., 2014), highlighting the importance of local climatic factors.

Adaptations for seed dispersal as a proxy for dispersal limitations, on the other hand, responded similarly to the investigated environmental variables (Table 3 section B). Dispersal limitations were thus likely not critical in influencing the relative importance of patch size versus isolation. No inselberg included in this study harboured species restricted to a particular inselberg. Thus if dispersal limitations were an important factor, then more species with short-range dispersal would be expected on isolated inselbergs. This was not the case. Insufficient data or scale are likely not factors explaining these patterns. Inselbergs were sufficiently isolated (nearly half were over 10 km from the nearest similar habitat) and dispersal categories were evenly distributed amongst the species. This means dispersal ability is indeed not critical in determining distribution of inselberg specialists in this study. There could be two reasons for this. (1) Inselberg specialists with short-range dispersal maintain viable populations on inselbergs, even if isolated beyond dispersal capacity from the nearest suitable habitat. (2) Adaptations for seed dispersal do not adequately reflect actual dispersal events. This has been demonstrated in several studies. These showed that occasional long-range dispersal events, even by species not adapted for long-range dispersal, can result in establishment of new populations which remain for long periods (Cain et al., 2000). Similarly such events could also maintain gene-flow (Millar et al., 2013).

4.5. Are there differences between species?

To understand underlying ecological mechanisms (in this study relative importance of patch size versus isolation), data from several species occurring in a particular habitat are usually amalgamated, whereas each species responds differently to the challenges imposed by a particular habitat (Grime, 1979). Zooming in on species level therefore helps to better understand these general patterns. The species-level analyses in this study generated the strongest correlations with the selected environmental variables, which is expected. When more species are included in an analysis, the variability between species in response to environmental variables weakens the overall correlation (Austin, 2002). Although only 15 inselberg specialists were sufficiently frequent across all inselbergs to allow statistical analyses, these provided some insights. All species responded differently to the investigated environmental variables (Table 4), irrespective of life form and dispersal adaptation. This supports the overall detected pattern of low influence of the investigated species traits on the effect of patch size and isolation.

Five of the investigated fifteen species (the shrubs *Abutilon pycnodon,* and *Helichrysum tomentosulum* and *Heliotropium steudneri*, the stem-succulent *Commiphora saxicola* and the tree *Sterculia africana*) showed significant, modest correlations with distance to mainland. Level of isolation may thus be a factor influencing their distribution in this arid inselberg landscape. *Commiphora saxicola* and *Helichrysum tomentosulum* could be dispersed over longer distances, as the one is animal-, the other wind-dispersed. But *Abutilon pycnodon, Heliotropium steudneri* and *Sterculia africana* have no particular adaptations for seed dispersal. Seed dispersal syndromes can therefore not explain this pattern.

These patterns, in combination with the fact that the tree life form also seemed to be affected by distance from source, strengthens the notion that level of isolation may be more important than area in determining some species distributions on Namib inselbergs. As discussed above, distance from mainland also presents a rainfall gradient in this study. Whether it is spatial distance per se or a combination of factors requires further investigation.

5. Implications for conservation and future research

This study corroborates the notion that applying island biogeographic concepts (i.e. a simplistic view of 'islands' of suitable habitat in a matrix of unsuitable habitat) to a terrestrial situation needs to be reevaluated (Laurance, 2008). The nature of the 'matrix', i.e. the areas surrounding the site under investigation (Prugh et al., 2008) needs to be considered. Also other environmental and intrinsic factors need to be included and applied to the specific environmental setting to achieve effective conservation of the landscape/habitat or species to be protected (Koh et al., 2010). Both landscape-level and species-level approaches are required to provide the appropriate context for effective conservation measures (Pearson et al., 1999). The protection of a particular species must take the species' needs into account (Shepherd and Brantley, 2005; Neel, 2008), and cannot rely solely on general biogeographic patterns (Wilson and Chiarucci, 2000).

Irrespective of size or isolation, inselbergs in an arid environment greatly contribute to enhancing species richness and serve as refugia to recolonise degraded rangelands in their surroundings. Altitudinal gradients have also been considered to buffer the effects of climate change (Bond and Richardson, 1990), and protecting inselbergs as 'source pools' would increase the chances of persistence of lowland populations in peril. Although this study focussed on inselberg specialists (i.e. species not occurring in lowlands), previous studies clearly showed their importance as sources of rangeland species which could re-colonise degraded areas from inselbergs (Burke et al., 2003). This is not only relevant in the Namib Desert and South Africa (Hoffman and Rhode, 2010) but also in North Africa (Anthelme et al., 2011), Australia (Hunter, 2003; Millar et al., 2013) and elsewhere. Inselbergs' contribution to the biodiversity of a landscape by providing habitat heterogeneity (Garrick, 2011) is thus unquestioned. The inselbergs in this study also support many species endemic to inselberg and mountain habitats in Namibia as well as red-listed species which further strengthens their importance for plant conservation.

Species richness of the arid Namib inselbergs compared very favourably with semi-arid inselberg landscapes, for example in eastern Australia, where under more than double the rainfall regime, granite inselbergs supported a mean of 22 species (Michael and Lindenmayer, 2012), compared to similar-sized granite and basalt inselbergs in the Namib, where 41–80 inselberg specialists (excluding generalists) were recorded. The reasons for this could be related to the overall poorer species pool on the Australian continent compared to the Namib's proximity to one of the world's richest floras (Linder, 2005; Cowling et al., 2009). But it could also be related to historical factors or reflect the intermediate status of semi-arid inselbergs on an arid to tropic gradient from species-rich to species-poor (Burke, 2003b). Whatever the reasons, the comparatively high species richness of Namib inselbergs further highlights the importance for their protection.

Adequate protection of these inselbergs is therefore important. This is presently the case in the Ganab and Namibrand landscapes, but not necessarily in the Spitzkoppe–Twyfelfontein and Etendeka–Barab landscapes, where livestock farming and small-scale mining impact inselberg vegetation. Another important threat to inselbergs is potential large-scale mining. Although inselberg specialist species richness appeared not affected by land-use (i.e. livestock farming) at a landscape level, the effect on the vegetation and species composition was not addressed in this study. In this context species richness on its own is not a sufficient indicator to evaluate impacts on vegetation and needs to be accompanied by other indicators (Sullivan and Rohde, 2002). Small-scale mining as well as exploration take place in some Namib inselberg landscapes and appropriate management of these impacts is crucial to ensure that the 'source pool' potential of inselbergs to recolonise impacted areas is not eroded.

As so often, this study raised further questions regarding the factors determining species richness of arid inselbergs. Vegetation and evolutionary history are some of the aspects which were not investigated and phylogenetic studies should therefore be considered in future to close some knowledge gaps. Also more detail with regard to the 'matrix' surrounding the inselberg 'patches' could possibly contribute useful insights (Prugh et al., 2008). Understanding these factors would help to identify vulnerable areas in need of higher protection due to human impact or climate change.

6. Conclusion

The analyses in this study mirrored the complexity of nature. At a landscape level, overall there was no clear indication that isolation is relatively more important than patch size in determining plant species richness on arid inselbergs. Species composition on inselbergs mirrored this complexity and also did not produce clear patterns in floristic relationships which could be attributed to one or several of the investigated environmental variables. However, when investigated at a functional and species-level, distance to mainland (or source pool, which is one proxy for the inverse of isolation), showed to be of greater importance than area for trees and also for selected species of trees, shrubs and stem-succulents. However, the effect of distance to source in this study is likely a function of spatial distance as well as a coast-inland moisture gradient and thus needs to be seen in this context. Rock type, which is a reflection of physical and chemical properties of the substrate influenced inselberg specialist-richness. The investigated environmental variables influenced the response of life forms of inselberg specialists. Dispersal limitation, however were not affected irrespective of the environmental variables.

The importance of inselbergs in arid landscapes as 'hotspots' of species richness which support range-restricted and red-listed plants is nonetheless indisputable. Inselbergs could also serve as a source pools of plants to re-colonise areas degraded due to grazing, climate change or other human impacts.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.sajb.2019.08.029.

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