Are Namibian inselbergs conservation islands? A floral perspective

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Plant communities and plant species diversity of four Namibian inselberg landscapes were investigated across the Nama Karoo biome to elucidate biogeographical patterns, the role of inselbergs as refugia of plant species, and environmental variables determining local and regional species patterns in inselberg landscapes. The inselbergs investigated are conservation islands with a high 're-colonization potential' and biodiversity value and contribute to regional and landscape-level species pools. Linkages between inselbergs and their surroundings existed in the form of gene flow and nutrient flow from inselbergs to lowlands. Exchange of species with similar habitats in the surrounding areas was important in the formation and maintenance of distinct inselberg plant communities. Stable communities with longer-lived species grew on granite inselbergs, whereas dolerite inselbergs supported transient communities comprised of short-lived species. At a regional level, climatic parameters influenced inselberg–matrix relationships. Floristic relationships between inselbergs were largely determined by geographical position and geology. Landscape-level variables were more important in governing functional relationships, and highlighted the importance of altitude as an environmental variable. There was also a link between the overall species pool and that of inselberg specialists. Linkages with potential mainland habitats differed depending on lithology and landform. Granite inselbergs showed closer links to potential mainland habitats than dolerite inselbergs. The conservation of groups of inselbergs rather than isolated mountains may be critical where inselbergs are a long way from potential mainland sources. Linkage corridors or 'stepping stones' from inselbergs to potential mainland sources are important, particularly for the conservation of taxa with short dispersal ranges.

Introduction

Species diversity and richness are determined by factors operating at different spatial[1] and time scales.[2] At a local level, niche relations and microhabitat are of importance, whereas the effect of neighbouring species pools contributes to diversity at a landscape-level.[3] Historical factors and geographical features, through long-term evolutionary processes, as well as the short-term effects of disturbance, can also influence species diversity.[4–6] Landscape features that provide environmental conditions slightly different from the overall surrounding conditions — for example, dry rivers and mountains in arid plains — are believed to allow species to persist in habitats and landscapes beyond their normal distribution ranges.[7] In addition, important rangeland species in decline on arid plains as a result of degradation may also find a home in these special habitats. Against the background of global climate change and increasing pressures on arid landscapes, this concept may have important implications for conservation planning and the maintenance of rangelands. Classical island biogeography provides the theoretical background against which hypotheses can be tested.[8,9]

The findings I present here are the result of four years of botanical surveys on inselbergs in the Namibian Nama Karoo (as part of an European Community project) and deal with biogeographical patterns, the role of inselbergs as refugia of plant species, and environmental variables determining local patterns in inselberg landscapes.

Methods

The survey methods, data analysis, and general characteristics of the inselbergs studied have been presented in detail elsewhere;[10–12] I give only a brief summary of the main parameters here.

Four inselberg landscapes in Namibia's Nama Karoo were investigated. These included four basalt mesas at Etendeka in northwest Namibia (approximately 19°S and 14°E), three granite inselbergs and six dolerite ridges at Spitzkoppe (approximately 21°S and 15°E), the Brukkaros mountain and three shale mesas (approximately 25°S and 17°E), and three gneiss inselbergs and two sandstone mesas in the vicinity of Klein Karas (approximately 27°S and 18°E). Three areas fall within the annual mean rainfall contour of 50–100 mm; the Brukkaros study area falls within the 100–200-mm rainfall contour.[13] The study areas span across an approximately 1000-km transect from northwest to southern Namibia.

Results and discussion

Local patterns

Although, as expected, plant communities different from those of the surrounding plains were found on Namibian inselbergs, boundaries between vegetation types were not clear, indicating a gradual transition from plain to inselberg communities.[14] As a result of these gradual transitions and the likely influence of parameters operating at landscape and regional scales, environmental parameters operating at the local level, for example, soil properties, emerged as poor descriptors of local patterns.

When investigated in isolation, however, soil properties of inselbergs showed some trends.[15] Parent material played an important role in determining soil

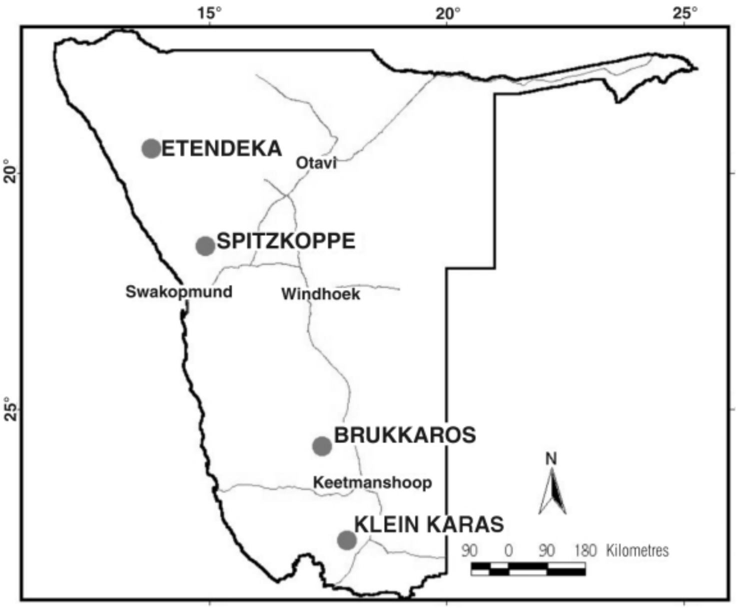

Fig. 1. Study area in Namibia with main roads and towns indicated.

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Table 1. Characteristics and plant species richness of investigated Namibian inselbergs.

	Etendeka	Spitzkoppe		Brukkaros		Klein Karas	
Characteristics							
Geology	Basalt	Granite	Dolerite	Breccia	Shale	Gneiss	Sandstone
Elevation range	210–500	220–390	10–240	530	105–140	90–140	70–210
n	4	3	6	1	3	3	2
Study area as % of Namibian land surface	1	3.3		1		0.05	
Total plant species (recorded)							
Mean and s.d. per inselberg	122 ± 24.3	125.7 ± 21.4	48.8 ± 20.3	168	64.7 ± 19.3	73.3 ± 9.5	79.5 ±19.1
Total species on inselbergs	211	193	123	168	98	109	109
Total species recorded in study area (% of Namibian flora)	220 (5%)	276 (6.4%)		211 (4.8%)		240 (5.5%)	
Inselberg specialists (recorded)							
Mean and s.d. per inselberg	55.3 ± 17.3	40.7 ± 5.9	8.6 ± 7.2	73	8.7 ± 5.8	22 ± 3.4	17.5 ± 4.9
Highest per inselberg	79	45	21	73	12	26	21
Namibian endemics (recorded)							
Total on inselbergs	38	39	23	22	16	9	10

n = number of inselbergs; s.d. = standard deviation.

physical and chemical parameters, in line with results from other arid regions.[16,17] Soils derived from igneous rocks such as basalt and dolerite were the most fertile.[15] Topography and landform also affected soil properties; transport of some soil nutrients to the surrounding lowlands was indicated on several inselbergs. Similar processes have been documented in other semi-arid landscapes,[18,19] indicating that inselbergs may play an important role by feeding some soil nutrients to surrounding lowlands.

Inselberg–matrix relationships

Analysis of the floristic relationship between inselbergs and their surroundings showed that all inselbergs provided refuges for species of rangeland importance, indicating that a 're-colonisation source' potential exists.[12] Regarding functional properties of species shared between plains and inselbergs, regional differences were found between dispersal spectra, but not in growth forms. These discrepancies were interpreted as being largely the result of differences in regional species pools — the phytogeographical composition of the surrounding flora — and not the result of differences in nature of the inselbergs *per se* (such as elevation or geology). Floristic affinities between plain and inselberg plant communities were clearly affected by geographical position, as well as distance to potential mainland habitat (nearest mountain habitat). Inselberg plant communities in southern Namibia, in an inland position and at a distance from potential mainland habitats, were more similar to plain communities than those further north, closer to the coast and closer to potential mainland sources.[11] These trends indicate that exchange with plant communities of similar habitats may be important in the formation of distinct inselberg communities.[20] In addition, broad climatic parameters such as more continental conditions in the south, and perhaps the occasional influence of fog in the northern study areas, could influence inselberg–matrix relationships. Northern inselberg communities were more distinct, whereas those in the south were more similar to plain communities. This would make inselbergs in the south 'better' sources for re-colonisation, but those in the north could be of greater importance to maintaining remnant populations adapted to different habitats and thus enrich landscape and regional species diversity.[21]

Relationships between inselbergs

Floristic relationships between inselbergs were mainly influenced by geographical position, secondly geology and then other factors related to the nature of inselbergs and surrounding landscapes.[10] In the southern study areas the distance between inselbergs also influenced floristic relationships: it showed a negative correlation, implying that floristic similarities declined with increasing distance between inselbergs. This trend is to be expected according to classic island biogeography.[8,9] Hence in landscapes where the influence of potential mainland sources is lessened, exchange of species between similar habitats may become more important in maintaining inselberg communities. Regarding growth form and dispersal spectra, functional relationships between different inselbergs, environmental variables operating at a landscape-level appeared more important than regional level parameters such as geographical position. Linkages with potential mainland areas differed depending on lithology and landform, with granite inselbergs showing closer links to the mainland than dolerite inselbergs (MS in prep.).

Species richness and conservation value of inselbergs

In contrast to some inselbergs in tropical areas,[22,23] none of the inselbergs in this study harboured plant species endemic to particular mountains. However, many of the recorded species are restricted to mountain habitats.[24] Basalt mesas, granite domes and the Brukkaros inselberg (breccia) harboured the highest number of 'inselberg specialists' (species restricted to inselberg habitats), and higher mountains were more likely to support these. The average number of inselberg specialists decreased in the order basalt mesas > breccia mountain > granite domes > gneiss domes > sandstone mesas > shale mesas and dolerite ridges (Table 1). This order was slightly rearranged when the total number of plant species was considered; these decreased in the order breccia mountain > granite domes > basalt mesas > sandstone mesa > gneiss domes > shale mesas > dolerite ridges (Table 1). Hence trends at the lower end of the scale were the same between total species numbers and number of inselberg specialists, but some switching of positions occurred at the upper end of the scale. These data, analysed according to area and geology, indicated some trends, but could not isolate regional influences (for example, differences in phytogeographical region between study areas) from landscape-level variables (such as geology and landform), and could therefore not be used to pinpoint the source of variation in species diversity patterns.[25]

However, the overall similarity between the arrangement of total species and inselberg specialists indicates that there may be a link between the overall species pool and the number of inselberg specialists. The number of inselberg specialists was linearly correlated to elevation, but not to surface area,[24] demonstrating that different microclimatic conditions, (for example, cooler temperatures and better moisture supply related to the effect of altitude) may be more important than the provision of inselberg habitat *per se.* Distance to escarpment was another important variable influencing the number of inselberg specialists.

When one particular landform of inselberg — mesas — was investigated across the entire Nama Karoo from Namibia to South Africa, an interesting trend emerged: at approximately 240-m elevation a change from plant communities more similar to the surrounding matrix (greater 're-colonisation source' potential) to more distinct inselberg communities (i.e. 'remnant function') occurred.[27] This conclusion further supports the view that at a landscape-level, higher mountains may well add to greater species diversity.[26]

Considering species richness in relation to the size of the study areas, the Klein Karas area had the highest species richness (Table 1). However, when based on the number of Namibian endemics and inselberg specialists, Klein Karas ranked lowest; here the plains contributed to higher species numbers, rather than the inselbergs, in contrast to the other study areas. In a national context, it is evident that inselberg landscapes make a significant contribution to species richness when considered in relation to surface area. The inselberg landscapes in this study covered 0.05–3% of the land surface, but the species richness ranged from 4.8–6.4% of the Namibian flora (Table 1). Considering that species richness is likely to be higher if studied over a longer period, owing to seasonal influences in this arid area, these landscapes provide a remarkable contribution to floral species diversity.

Implications for conservation planning

Nama Karoo inselbergs can be considered conservation islands with a high 're-colonisation potential' and biodiversity value, and contribute to both regional and landscape-level species pools.

Linkages between inselbergs and their surroundings exist in the form of gene flow, as well as likely nutrient flow from inselbergs to lowlands. In these arid landscapes, exchange of species with similar habitats in the surrounding areas is important in the formation and maintenance of distinct inselberg plant communities. Stable communities with many long-lived species grow on granite inselbergs, whereas dolerite inselbergs support transient communities comprised largely of short-lived species.

At a regional level, climatic parameters —such as more continental conditions in the south and, possibly, the occasional effect of fog in the northern study areas —influence inselberg–matrix relationships. Floristic relationships between inselbergs are largely determined by geographical position and geology. Landscape-level variables are more important in governing functional relationships; this highlights the importance of altitude as an environmental variable.

There is also a link between the overall species pool and that of inselberg specialists. Linkages with potential mainland habitats differ depending on lithology and landform. Granite inselbergs show closer links to potential mainland habitats than dolerite inselbergs.

The conservation of groups of inselbergs rather than isolated mountains may be critical where inselbergs are a long way from potential mainland sources. Linkage corridors or 'stepping stones' from inselbergs to potential mainland sources are important, particularly for the conservation of taxa with short dispersal ranges. Species richness and surface area covered in relation to national statistics may be useful in developing indicators to identify areas of high conservation priority.

I am indebted to my husband for invaluable assistance during the field work for this project. Phoebe Barnard and the Namibian National Biodiversity Programme provided logistic support; a European Community grant (ERBIC18CT910141) provided financial support.

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