Evolutionary Ecology Research, 2007, **9**: 283–297

Plant endemism in the central Namib Desert

Antje Burke*

EnviroScience, PO Box 1722, Oranjemund, Namibia

ABSTRACT

Questions: Have Namib endemics evolved from old or recent evolutionary lines? What are their phylogenetic patterns at different levels of taxonomic order? What is the role of environmental factors in determining current distributions?

Data description: Distribution of central Namib plant endemics and environmental indices, based on field surveys and published sources.

Method of analysis: Chi-squared and *G*-tests to examine differences in phylogenetic aspects, growth form, and dispersal spectra between endemic and non-endemic flora. Canonical correspondence analysis to investigate the effect of environmental variables on the distribution of plant endemics in a 15-minute interval geographic grid.

Conclusions: Central Namib endemics have probably descended from old evolutionary lines in contrast to those in the southern Namib. Different selective forces are therefore likely to be driving evolution in different parts of the Namib Desert. Although leaf-succulents are over-represented among both central Namib and southern Namib endemics, leaf-succulents in the central Namib are likely to be a result of former environmental conditions (i.e. winter rainfall) and/or the influence of fog, in contrast to the southern Namib where phylogenetics play a more important role. Species-specific responses are indicated among the Namib endemics, as the influence of fog seems to be important for some, and substrate conditions for others. These need to be taken into account when predictions are made regarding broad-scale biogeographic patterns and when modelling the effect of climate change.

Keywords: arid lands, biogeography, climate change, evolution, growth forms, southern Africa.

INTRODUCTION

The Namib Desert straddles southern Africa's west coast and is considered one of the oldest deserts in the world (Ward *et al.*, 1983). During a long history of evolution, plants and animals have hence adapted to these arid conditions. Endemism is high among insects, in particular ground-dwelling insects, such as tenebrionids (Tenebrionideae) (Louw, 1983) and scarabs (Sole *et al.*, 2005), as well as among reptiles (Branch, 1988; Griffin, 2000), but little is know about plant endemism in this ancient desert.

Two contrasting climate regimes reign in the Namib Desert. The very south is within the influence of the southern hemisphere's temperate cyclone system and receives winter rains

* e-mail: antje@enviro-science.info

regularly. The vegetation there is typical of southern Africa's succulent karoo biome (Burke *et al.*, 2002). The central and northern parts of the Namib Desert, however, fall within southern Africa's summer rainfall regime and the vegetation is characterized by ephemeral grassland and localized patches of shrubland (Jürgens *et al.*, 1997). Because of these different environmental conditions, the driving forces and time frames for evolution within the central and northern Namib flora likely differ from that of the southern Namib. Vegetation history, influenced by past climatic conditions, ecology, and genetic adaptations – each factor varying in intensity depending on the particular situation – are believed to be the major causes of endemism (Kruckeberg and Rabinowitz, 1985). The importance of paleoclimatic fluctuations driving endemism in the Cape flora of southern Africa has been stressed (e.g. Linder, 2001; Midgley *et al.*, 2001), while in the succulent karoo in particular, rocky, stable substrates are hypothesized to favour the development of endemic plants (Desmet and Cowling, 1999). The evolution of one of the dominant groups of plants in the succulent karoo, the Mesembryanthemaceae, is believed to be a very recent phenomenon (Klak *et al.*, 2004) and an analysis of southern Namib plant endemics confirms this pattern (Burke, 2005). Preliminary analysis of the entire Namib flora, however, indicated that, based on the low number of species per genus, speciation was probably an old rather that a recent phenomenon (Robinson, 1978). Regarding evolutionary patterns, a differentiation may have to be made between the southern Namib on the one hand and the central and northern Namib on the other. A more detailed analysis of the central Namib flora in this regard is lacking at present.

A recent study predicted that the impacts of climate change on endemic plants in Namibia could be less severe than on other plants, because of their adaptation to an arid environment (Midgley *et al.*, 2005). This hypothesis deserves some attention. Investigating plant functional attributes of endemic plants as well as their correlation with environmental factors will provide more information to help test this hypothesis. Understanding patterns and trends among endemics is critical to devise appropriate conservation strategies. Therefore, are trends found in the southern Namib flora also applicable to the central Namib? Particular questions posed in this study include:

- Have Namib endemics ascended from old or recent evolutionary lines? For example, what are their phylogenetic patterns at different levels of taxonomic order?
- How have Namib endemics adapted to this environment in terms of plant functional traits, are particular growth forms over- or under-represented, and what are the endemic plant's seed dispersal characteristics?
- What is the possible role of environmental factors driving the development of endemic species?

Distribution patterns and functional traits of Namib endemics growing in the central Namib Desert are investigated in this study with the aim of helping to answer these questions.

METHODS

Study area

The Namib Desert has been divided into four major parts based on climatic regime and substrate. Jürgens and colleagues (1997) distinguish from north to south the northern Namib,

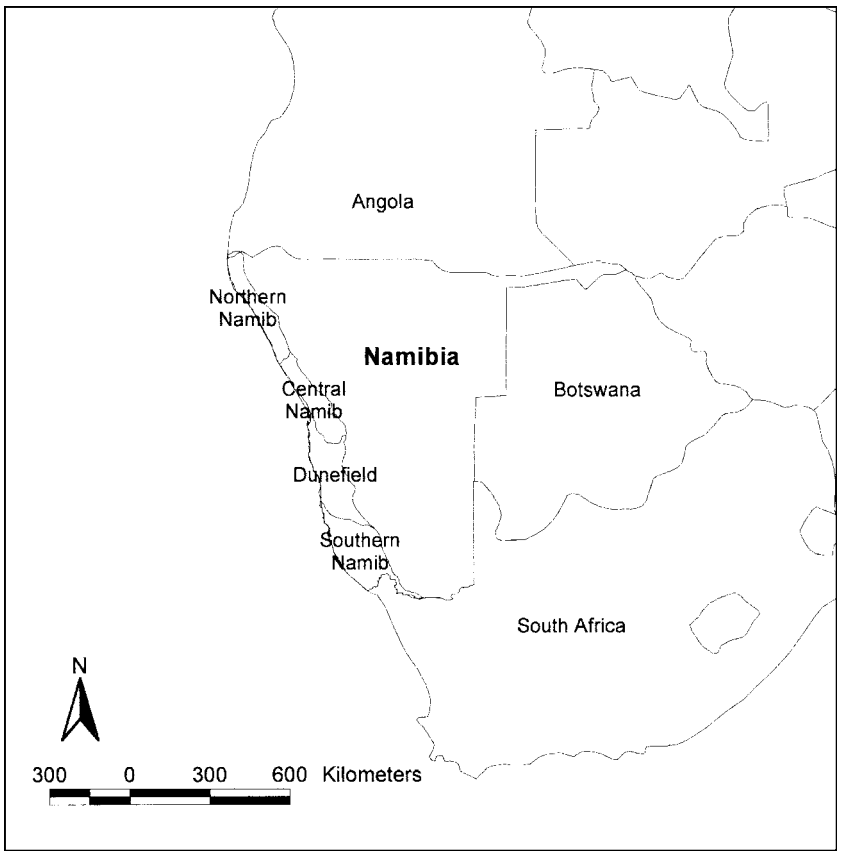

Fig. 1. Position of the central Namib Desert in southern Africa.

central Namib, central Namib dunefield, and southern Namib (Fig. 1). For the purpose of this study, the definition of the central Namib followed the classification of Giess (1971) and was defined as stretching from the Kuiseb to the Huab River. The eastern boundary is the escarpment in the Namib-Naukluft Park section of the central Namib. Where the escarpment shows a natural break, the boundary runs at 22° latitude south from about 15° longitude east diagonally in a northwest direction to about 14° longitude east at 20°45′ south. It therefore excludes the Brandberg and Erongo Mountains and the Spitzkoppe inselbergs (Fig. 2). The area covers 23,000 km^2 and is characterized by vast plains, intersected by drainage lines and depressions and occasional isolated mountains (inselbergs) and ridges. Rainfall increases west (coast) to east (inland) from about 15 mm annual average at the coast to some 85 mm inland [e.g. at Ganab in the Namib-Naukluft Park (Lancaster *et al.*, 1984)]. Fog is another important source of moisture, which, in contrast to rainfall, decreases from the coast to about 30 km inland. Fog precipitation can reach a remarkable 180 mm per annum on rocky outcrops near the coast (Lancaster *et al.*, 1984), and Nagel (1962) estimated that plants intercept the equivalent of a mean 150 mm rainfall per annum at the coast. However, on the central Namib plains, a maximum of 64 mm, decreasing to about 20 mm, fog precipitation was recorded along a coast–inland gradient

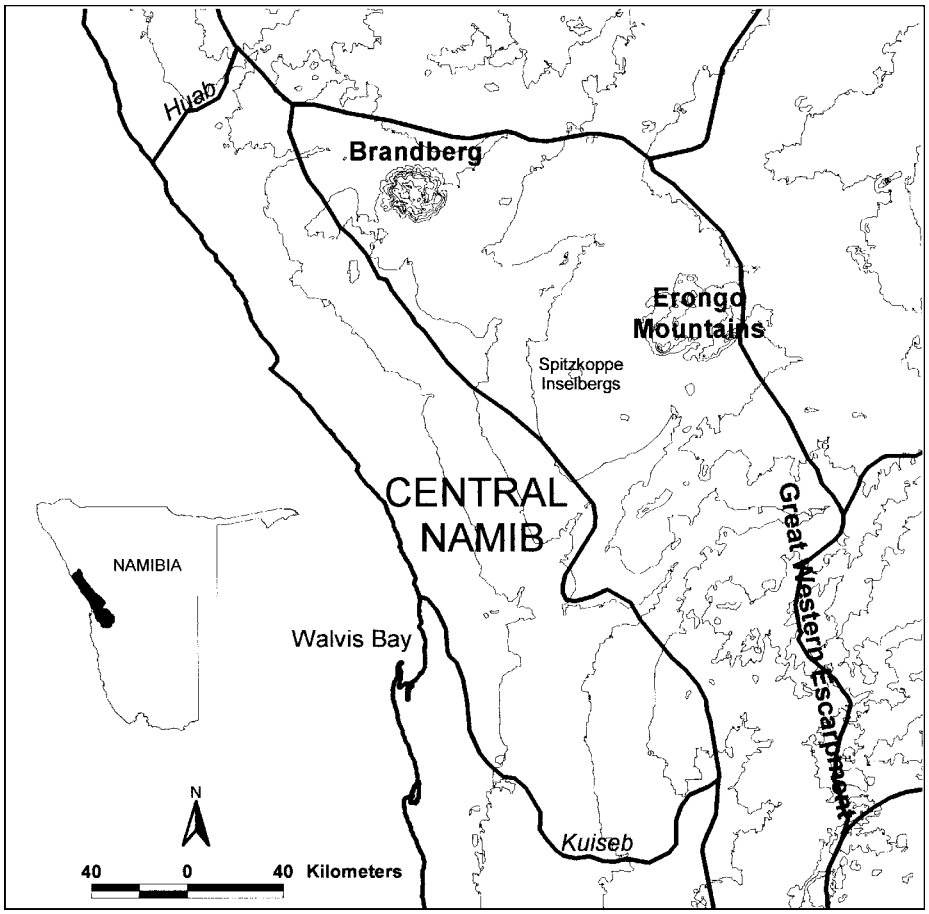

Fig. 2. Study area in Namibia and 150–300 m altitude contours.

in the fog belt (Hachfeld and Jürgens, 2000). The vegetation is classified as dwarf shrubland (Burke *et al.*, 2002), showing low but continuous cover in the Namib fog belt but contracting in drainage lines and depressions in the inland areas (Walter, 1986). The soils are either gypsum- or calcium-rich (gypsisols or calcisols) (Scholz 1972), very shallow regosols on rock outcrops (Burke, 2002) or dune sands.

Data analysis

A species list of the central Namib was compiled based on 15 years of research and collecting by the author, herbarium records for endemic species, as well as published sources (Robinson, 1976; Theron *et al.*, 1980; Giess, 1981; Nel, 1983; Günster, 1992; Hachfeld, 2000; Craven, 2002). Two levels of endemism were investigated: (1) Namibian endemics and (2) Namib endemics. *Namibian* endemics were defined as endemic to within Namibia's political borders, whereas *Namib* endemics were defined as mainly restricted to within the boundaries of the Namibian part of the Namib Desert [more than 50% of their distribution within the boundaries of the northern, central, and southern Namib Desert as defined by Giess (1971)]. This distinction

was made to separate factors that may have operated at the Namibian level and those that were likely restricted to the Namib Desert. Although the Namib Desert extends northwards into Angola, distribution records for the Angolan part of the Namib are scarce and this area was thus excluded from the analysis.

G-tests and 2×2 chi-square tables (Fowler and Cohen, 1992) were used to test for differences between endemics and non-endemics in terms of phylogenetic aspects and plant functional attributes such as growth form, succulence, and seed dispersal. The Yates correction factor (Fowler and Cohen, 1992) was applied in all chi-square analyses. These tests were carried out for Namibian endemics as well as Namib endemics. Statistical significance was set at $P < 0.05$ for all analyses. Growth form categories included in this analysis were dwarf stem succulents (≤ 10 cm), evergreen plants, grasses, geophytes, annual herbs, leaf-succulents, deciduous shrubs, stem-succulents (> 10 cm), trees, and ferns. A further test was performed to distinguish between succulent (tissue water-storing) and non-succulent species. Based on morphological adaptations (van der Pijl, 1969), the following seed dispersal categories were included: wind, water, ballistic, animal, and no particular vector. The dual dispersal strategies wind and water, as well as wind and animals, were also accounted for.

Correlations between the distribution of Namib endemics and broad-scale environmental variables were explored through canonical correspondence analysis (CCA). The computer program Canoco 4 for Windows was employed for this purpose (ter Braak and Smilauer, 1998) using the default setting (no data transformation, no down-weighting or selection of species) and applying Monte Carlo permutation tests. The resolution of the data is quarter degree squares (15-minute intervals of a latitude–longitude grid which were treated as samples). Twenty-one Namib endemic species and 150 quarter degree squares were included in the analysis. Environmental variables comprised fog, rain, water deficit, and two parameters of the substrate – stability (stable or mobile) and special chemical conditions (gypsum-rich, calcium-rich or neither). Background data available at a national level (Mendelsohn *et al.*, 2002) were used to derive values per quarter degree square. For this purpose, indices of (1) fog frequency (number of days of fog per annum), (2) annual average rainfall, and (3) water deficit (difference between average annual rainfall and average evaporation) were developed per quarter degree square. These indices were computed by multiplying the percent cover per quarter degree square that a particular range of values covered with the median of this particular range. Substrate parameters derived from a soil map (Mendelsohn *et al.*, 2002) were coded as nominal data, whereby stability of the substrate was defined as mobile if more than 50% of the relevant quarter degree square was covered by mobile dunes, and all other substrates were defined as stable. Special substrate conditions are expected to occur linked to calcrete and gypsum soils (Scholz, 1972; Blümel, 1982). Because of their often localized distribution, where more than 25% of a quarter degree square covered either gypsicols (gypsum soil) or calcisols (calcareous soil), these were coded as such.

RESULTS

Of the 410 species that occur in the central Namib and included in this analysis, 88 were confined to within the borders of Namibia, thus 21.5% are Namibian endemics. However, only 21 of these were Namib endemics – restricted to the Namibian part of the Namib Desert – comprising 5.1% of the central Namib flora (Table 1). These include a number of grasses (e.g. *Eragrostis pygmaea*, *Stipagrostis namibensis*, *S. seelyae*), succulent herbs (*Aizoanthemum rehmannii*), dwarf shrubs (*Arthraerua leubnitziae*, *Zygophyllum*

Table 1. Ranges and number of endemic plant species in the central Namib Desert

Range	No. of species
Namib	21
Namib and escarpment	21
Namib and central Namibia	10
Namibia	36
Total	88

stapffii), herbs (e.g. *Anticharis ebracteata*, *Helichrysum marlothianum*, and *Hermbstaedtia spathulifolia*), and one geophyte (strictly speaking a hemicryptophyte, *Raphionacme haeneliae*). Based on current distribution records, only three species were confined entirely within Giess's (1971) central Namib boundaries: *Helichrysum marlothianum*, *Lithops ruschiorum*, and *Raphionacme haeneliae*. Some Namib endemics extend their range eastwards in the Brandberg area. These include, for example, *Aloe asperifolia* and *Aloe namibensis*. However, another two species not entirely confined to the Namib Desert were included as Namib endemics. The dune grass *Stipagrostis sabulicola* has established some small outlier populations on mobile dunes in the south of Namibia, while an isolated population of the herb *Senecio engleranus* occurs in the Auas Mountains in central Namibia.

Phylogenetic patterns

The number of species per family did not differ significantly between Namibian endemics and non-endemics ($G = 21.09$, d.f. = 27, $P > 0.05$). Non-endemic species were distributed across 71 families and endemic species across 31 families. Two families contained endemics but had no non-endemic counterparts – Passifloraceae (*Adenia pechuelii*) and Tecophilaceae (*Cyanella amboensis*). Regarding the number of genera per family, there was no significant difference between Namibian endemics and non-endemics ($G = 10.96$, d.f. = 27, $P > 0.05$). The same result was observed for number of species per family for Namib endemics, with no significant difference between Namib endemics and non-Namib endemics ($G = 13.31$, d.f. = 10, $P > 0.05$).

Plant functional attributes of endemics

There were significant differences in growth forms between Namibian endemics and non-endemics ($G = 19.84$, d.f. = 8, $P < 0.05$), with evergreen plants ($\chi^2 = 3.87$, $P < 0.05$) and trees ($\chi^2 = 6.41$, $P < 0.05$) being under-represented among the endemics. When differences in growth forms were tested between Namib endemics and non-Namib endemics (including Namibian endemics), significant differences were again observed ($G = 13.07$, d.f. = 4, $P < 0.05$), but this time there was an over-representation of leaf-succulents ($\chi^2 = 8.01$, $P < 0.01$).

With regard to succulent plants growing in the central Namib, there were no significant differences in succulence between the Namibian endemics and non-endemics ($\chi^2 = 2.49$,

Table 2. Number of succulent and non-succulent plant species for Namib endemics and non-Namib endemics in the central Namib

	Succulent	Non-succulent
Namib endemics	9	21
Non-Namib endemics	42	390

$P > 0.05$), but there were significantly more succulents among the Namib endemics ($\chi^2 = 10.4$, $P < 0.01$) than the non-Namib endemics (including Namibian endemics) (Table 2).

Seed dispersal spectra between Namibian endemics and non-endemics were not significantly different ($G = 12.55$, d.f. = 6, $P > 0.05$), as were seed dispersal spectra between Namib endemics and non-Namib endemics (including Namibian endemics) ($G = 2.70$, d.f. = 3, $P > 0.05$).

Distribution of Namib endemics in relation to environmental factors

The four canonical axes in the CCA explained a total of 83.3% of the species–environment variances. The Monte Carlo permutation tests showed that the first canonical axis was significant ($F = 6.38$, $P = 0.005$), as well as all axes tested together ($F = 2.63$, $P = 0.005$). This fact and the explained high cumulative percentage variance indicate that the selected environmental variables appear to be important in explaining species distributions. Total inertia summed up to 7.896 with individual eigenvalues of 0.34, 0.2, 0.12, and 0.09 for canonical axis 1, 2, 3, and 4 respectively.

Although the Namib endemic plants included in this analysis did not form distinct groups, some separation according to environmental variables was observed (Fig. 3). Stability of substrate was strongly correlated with the first canonical axis (correlation coefficient for mobile substrate = 0.813 and for stable substrate = −0.813), separating dune grasses (*Stipagrostis sabulicola* and *S. seelyae*) from all other plants. The occurrence of fog and quantity of rainfall were strongly correlated with the second canonical axis (correlation coefficient for fog = 0.808 and for rain = −0.809), as was gypsum substrate (correlation coefficient = 0.708). The negative correlation coefficient indicates that decreasing rainfall (i.e. aridity) played an important role here. Canonical axis 2 indicates that the distributions of *Lithops ruschiorum*, *Eragrostis pygmaea*, *Stipagrostis hermannii*, and *Euphorbia giessii* may rely on fog occurrence and/or gypsum substrates. At the opposite spectrum of axis 2, *Raphionacme haeneliae*, *Aloe namibensis*, *Aloe asperifolia*, and *Cleome foliosa* occur where there is higher rainfall and/or calcrete substrate.

DISCUSSION

With just over 5% of the central Namib flora restricted to the Namib Desert, richness of endemics ranks the central Namib fairly low compared with the exceptionally high level of endemism recorded in the succulent karoo biome (Cowling and Hilton-Taylor, 1999), other arid areas in southern Africa and around the world. Although richness of endemics may be relatively low, it is remarkable that some Namib endemics almost exclusively form the dominant

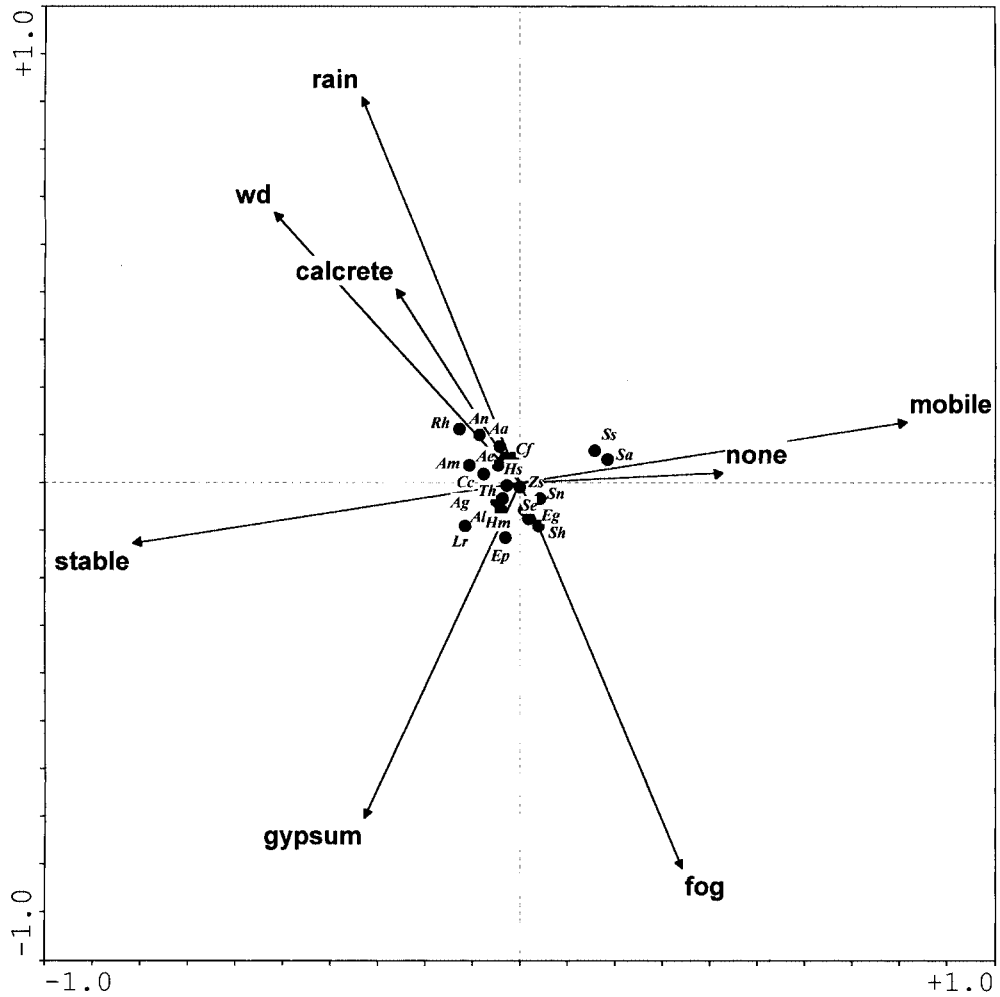

Fig. 3. Canonical correspondence analysis of Namib endemics that occur in the central Namib and environmental parameters (none = no special substrate conditions; wd = water deficit). Species abbreviations: *Aa = Aloe asperifolia*, *Ae = Anticharis ebracteata*, *Ag = Aizoanthemum galenioides*, *Al = Arthraerua leubnitziae*, *Am = Aizoanthemum rehmannii*, *An = Aloe namibensis*, *Cc = Cleome carnosa*, *Cf = Cleome foliosa* var. *namibensis*, *Ep = Eragrostis pygmaea*, *Eg = Euphorbia giessii*, *Hm = Helichrysum marlothianum*, *Hs = Hermbstaedtia spathulifolia*, *Lr = Lithops ruschiorum*, *Rh = Raphionacme haeneliae*, *Sa = Stipagrostis sabulicola*, *Se = Senecio engleranus*, *Sh = Stipagrostis hermannii*, *Sn = Stipagrostis namibensis*, *Ss = Stipagrostis seelyae*, *Th = Trianthema hereroensis*, *Zs = Zygophyllum stapffii*.

vegetation in large parts of the Namib Desert. This contrasts with other parts of southern Africa where endemics are often confined to localized areas (e.g. Desmet and Cowling, 1999; Schmiedel and Jürgens, 1999; Proches *et al.*, 2003; Ellis and Weis, in press). *Stipagrostis sabulicola* dominates the dune fields, while *Arthraerua leubnitziae* and *Zygophyllum stapffii* are the dominant vegetation in many parts of the Namib coastal plains within the fog belt.

The Great Western Escarpment, which has been linked to two separate geological events in Namibia (Aizawa *et al.*, 2000), appears to form an important geographic barrier for endemics. This is illustrated by an eastward extension of some Namib endemics in the Brandberg area. Here the lack of a clearly defined escarpment may have facilitated their distribution on plains eastwards.

Defining the geographic entity for a study of endemism invariably involves some bias, except where islands or other similarly clearly defined entities are investigated. In this case, there is no consensus regarding the definition of the Namib boundaries (Giess, 1971; Irish, 1994; Jürgens *et al.*, 1997), and the definition adopted in this study could be questioned. However, this was not expected to affect the general trends that emerged in the study.

Phylogenetic patterns

The same trends at the species and genus level were maintained for the Namibian endemics and Namib endemics that grow in the central Namib Desert. This indicates that in both instances their development is likely linked to old evolutionary lines and confirms the predictions of Cowling and Hilton-Taylor (1997) for the development of endemism among the southern African flora. Their subcontinent-wide study postulated that paleoendemics may be found in the western, arid parts of the subcontinent. Phylogenetically, the Namib endemics form a subset representative of the central Namib flora. This clearly contrasts with the southern Namib, where certain families are over-represented (Burke, 2005) and evolutionary development is considered to be recent (Ihlenfeldt, 1994; Klak *et al.*, 2004). Based on DNA analysis, Klak and colleagues (2004) confirmed that the speed of speciation in the family comprising the main component of southern Namib endemic flora (Mesembryanthemaceae or Aizoaceae) is unrivalled in the plant kingdom. Consequently, a large number of species per genus, or genera per family, are often linked to recent evolution.

Plant functional attributes of endemics

As indicated by examples from around the world, the functional attributes of endemic species are largely determined by environmental history, such as degree of isolation, adaptations to herbivory and soil conditions (Poot and Lambers, 2003), as well as recent climate (e.g. Hedberg, 1986; Harrison *et al.*, 2000; Grubb, 2003). As no particular genus or family is over- or under-represented among the endemics, trends in plant functional attributes are not affected by phylogenetics and thus considered largely adaptations to environmental conditions. Regarding growth form attributes, Namibian endemics in the central Namib show an under-representation of evergreen plants and trees, while no such trend emerged among the Namib endemics. However, Namib endemics showed an over-representation of leaf-succulents. This trend was confirmed by succulence showing no significant difference between Namibian endemics and non-endemics, but between Namib endemics and non-Namib endemics. In the central Namib, Namibian endemics are hence rarely evergreen plants or trees and Namib endemics are more likely to be leaf succulents. The lack of endemic trees in arid areas elsewhere in southern Africa has also been confirmed by an analysis of the flora of the entire subcontinent (Cowling and Hilton-Taylor, 1997). However, growth forms only provide a coarse surrogate of function, there are possibly overlapping traits, and physiological aspects, which would better describe function, have only been studied in a

few Namib endemic plants. More detailed studies are clearly required to shed light on functional aspects.

The over-representation of succulents among the Namib endemics is in line with findings from the southern Namib where compact leaf succulents show a remarkably high diversity among the endemics (Burke, 2005). Interestingly, while phylogenetics has contributed to the over-representation of leaf succulents in the southern Namib – all endemic compact leaf succulents are members of the family Mesembryanthemaceae – this appears not to be the case in the central Namib. Hence the over-representation of leaf-succulents among Namib endemics in the central Namib raises some questions. The high level of endemism among succulents in the succulent karoo biome, which includes parts of the southern Namib, has been largely attributed to the effects of winter rains, which provide climatically contrasting conditions to summer rainfall areas (e.g. Cowling and Hilton-Taylor, 1999). The central Namib is today positioned in the summer rainfall regime, but occasional winter rains are experienced here, as recorded at the Brandberg (Breunig, 1990) and at the Namib research station at Gobabeb. These occasional events may maintain a flora that originally evolved during winter rain conditions, when the southern hemisphere's temperate cyclone belt was positioned further north (Van Zinderen Bakker and Muller, 1987). Another explanation could be that fog, which provides a regular, low amount of moisture, favours the development of succulence. Succulents worldwide are generally found in areas where steady, low amounts of moisture are present all year round (Ellenberg, 1981; Burgess and Shmida, 1988; Grubb, 2003), which supports the findings of the present study.

The fact that seed dispersal spectra showed the same trend for Namib and Namibian endemics (no significant differences between spectra) points towards seed dispersal abilities not constituting a selective force among the endemics. However, seed dispersal classification based on morphological adaptations does not account for the actual process of seed dispersal and this may hence leave the process of actual dispersal undetected.

Distribution of Namib endemics in relation to environmental factors

Although, at a broad level, similar environmental factors may have been responsible for the evolution of endemic species in the central Namib, as indicated by the tight groupings of endemics in the canonical correspondence analysis, some species were separated from this cluster (Fig. 3), possibly linked to substrate properties and precipitation (occurrence of fog and decreasing rainfall). The influence of mobile substrates and fog on animal and plant life in the Namib Desert has been demonstrated repeatedly (Seely, 1978, 1991; Robinson and Seely, 1980). Whether both these factors could also be important selective forces driving endemism deserves further attention. The correspondence analysis in this study showed that the distribution of Namib endemics may be partially linked to fog, although here only measured in number of days of fog occurrence rather than actual amount (detailed data were not available in the resolution required for this study). The amount of precipitation delivered by fog greatly surpasses that of rainfall in the coastal region (Hachfeld and Jürgens, 2000) and can be as high as 180 mm per annum, as measured on isolated outcrops near the coast (Lancaster *et al.*, 1984). This corresponds to the amounts of rain received in the savanna regions to the east, and this could support a different suite of plants than the more arid inland parts of the Namib. The occurrence of fog is also linked directly to cooler temperatures and fewer hours of daily sunshine, which also affect plant growth. With regard to substrate properties, although undertaken at a coarse level, this study indicates that edaphic

properties could be important. Stability of the substrate and the occurrence of gypsum in particular, but also possibly calcrete, may influence the distribution of endemics such as *Eragrostis pygmaea* and *Stipagrostis hermannii*. Gypsum has been suggested to contribute to the development of the extensive lichen fields in the Namib Desert (Jürgens and Niebel, 1994), but whether there are gypsum-specialists among the Namib endemics needs to be investigated at a local scale. In arid regions elsewhere, edaphic conditions have often been considered to be primary causes for endemism (e.g. Desmet and Cowling, 1999; Camargo-Ricalde *et al.*, 2002; Poot and Lambers, 2003; Ellis and Weis, in press), and gypsum endemics, for example, are reported from arid regions in the Middle East (Akhani, 2004), Mojave Desert (Hickerson and Wolf, 1998), and Spain (Escudero *et al.*, 1999). A more detailed study of Namib endemics together with climate and vegetation history is critical for an interpretation of extant patterns of endemism (e.g. Midgley *et al.*, 2001; Grubb, 2003).

Implications

The results of this study suggest that species-specific responses are to be expected among some members of the Namib endemic flora. Hence models developed to predict centres of endemism in the arid Namib cannot necessarily assume homogeneity among all species. Species-specific models may need to be developed to avoid poor predictions of endemism based on area and other broad geographic parameters (Green *et al.*, 2003). This has also been demonstrated in the South American Andes recently (Kessler, 2002), where at a detailed level not all endemics in one area developed in response to the same environmental factors.

The occurrence of fog may be an important factor maintaining some Namib endemics. *Trianthema hereroensis*, for example, takes up fog water directly through its stomata (Nott and Savage, 1985), and although an unusual adaptation in an arid region, it has also been observed in the South American fog-influenced Atacama Desert (Walter, 1983). There are possibly other candidates in the central Namib showing the same adaptation, such as *Arthraerua leubnitziae*, although this has yet to be demonstrated.

Very little is known about the influence of climate change on fog patterns along the southern Africa West Coast, although impacts are likely. Should fog patterns be affected, so would endemics that rely on fog. Hence the hypothesis that Namib endemics may not be so severely affected by climate change as other plants in Namibia (Midgley *et al.*, 2005) needs some refinement on a species level.

CONCLUSIONS

The results of this study indicate marked differences in phylogenetic trends as well as some functional attributes between plant endemics in the central and the southern Namib, pointing towards different selective forces in the two parts of the Namib Desert. A study of Namibia's succulent karoo endemics (comprising the major part of the southern Namib) hypothesized that phylogenetic (genetics and history) and ecological factors (adaptations to external factors) may be of equal importance in the development of endemics in this area (Burke, 2005). As phylogenetics does not play a role in the development of central Namib endemics, adaptation to external factors is hypothesized to be the main driving force here. These factors likely include substrate properties, fog occurrence, and aridity. Separate analyses of floras often treated as one entity, such as in the case of the Namib Desert, might

hence be important in detecting underlying factors, which are otherwise masked by inappropriate scale of analysis and thereby prevent meaningful comparisons (Dungan *et al.*, 2002; Liebhold and Gurevitch, 2002).

Regarding growth forms, despite an apparent different evolutionary history in the southern and central Namib flora, leaf succulents were over-represented among endemics in both areas. Different factors could, however, have been the driving forces for this development – phylogenetics in the southern Namib, external factors such as possibly fog in the central and northern Namib.

Species-specific responses are indicated in some Namib endemics, as fog influence appears to be important for some and substrate conditions possibly for other species. Predictions based on broad-scale biogeographic parameters, as used in climate change models, need to take these differences into account.

ACKNOWLEDGEMENTS

Access to herbarium records held at the National Botanical Research Institute in Windhoek was essential for this analysis. The Ministry of Environment and Tourism of Namibia granted permission for collecting work throughout Namibia including National Parks, and the Ministry's field staff has been very supportive over the years. I would like to thank these institutions and their staff. Beryl Simpson provided valuable comments that greatly improved the manuscript.

REFERENCES

Aizawa, M., Bluck, B., Cartwright, J., Milner, S., Swart, R. and Ward, J. 2000. Constraints on the geomorphological evolution of Namibia from the offshore stratigraphic record. *Comm. Geol. Surv. Namibia*, **12**: 337–346.

Akhani, H. 2004. A new spiny, cushion-like Euphorbia (Euphorbiaceae) from south-west Iran with special reference to the phytogeographic importance of local endemic species. *Bot. J. Linn Soc.*, **146**: 107–121.

Blümel, W.D. 1982. Calcretes in Namibia and SE-Spain – relations to substratum, soil formation and geomorphic factors. *Catena*, **1** (suppl.), 67–82.

Branch, B. 1988. *Field Guide to the Snakes and Other Reptiles of Southern Africa*. Cape Town: Struik Publishers.

Breunig, P. 1990. Temperaturen und Niederschläge im Hohen Brandberg. *J. Namibia Sci. Soc.*, **42**: 7–24.

Burgess, T.L. and Shmida, A. 1988. Succulent growth forms in arid environments. In *Arid Lands: Today and Tomorrow* (E.A. Whitehead, ed.), pp. 383–395. Tuscon, AZ: University of Arizona Press.

Burke, A. 2002. Properties of soil pockets on arid Nama Karoo inselbergs – the effect of geology and derived landforms. *J. Arid Environ.*, **50**: 219–234.

Burke, A. 2005. Endemic plants of the arid succulent karoo in Namibia – towards hypotheses for their evolution. *Ecography*, **28**: 171–180.

Burke, A., du Plessis, W. and Strohbach, B. 2002. *Vegetation types in Namibia*. Supplementary data to Environmental Atlas of Namibia, Ministry of Environment and Tourism, Windhoek (available at: http://www.dea.met.gov.na/data/Atlas/Atlas_ web. htm#4Vegetation).

Camargo-Ricalde, S.L., Dhillion, S.S. and Grether, R. 2002. Endemic Mimosa species, community structure, and environmental heterogeneity in the semiarid Valley of Tehuacan-Cuicatlan, Mexico. *J. Veg. Sci.*, **13**: 697–704.

Cowling, R.M. and Hilton-Taylor, C. 1997. Phytogeography, flora and endemism. In *Vegetation of*

Southern Africa (R.M. Cowling, D.M. Richardson and S.M. Pierce, eds.), pp. 43–61. Cambridge: Cambridge University Press.

Cowling, R.M. and Hilton-Taylor, C. 1999. Plant biogeography, endemism and diversity. In *The Karoo: Ecological Patterns and Processes* (W.R.J. Dean and S.J. Milton, eds.), pp. 42–85. Cambridge: Cambridge University Press.

Craven, P. 2002. *Phytogeography of Namibia: a taxon approach to the spermatophyte flora*. MSc thesis, University of Stellenbosch, South Africa.

Desmet, P.G. and Cowling, R.M. 1999. Biodiversity, habitat and range-size aspects of a flora from a winter rainfall desert in the north-western Namaqualand, South Africa. *Plant Ecol.*, **142**: 23–33.

Dungan, J.L., Perry, J.N., Dale, M.R.T., Legendre, P., Citron-Pousty, S., Fortin, M.-J. *et al.* 2002. A balanced view of scale in spatial statistical analysis. *Ecography*, **25**: 626–640.

Ellenberg, H. 1981. Ursachen des Vorkommens und Fehlens von Sukkulenten in den Trockengebieten der Erde. *Flora*, **171**: 114–169.

Ellis, A.G. and Weis, A.E. in press. Coexistence and differentiation of 'flowering stones': the role of local adaptation to soil microenvironment. *J. Ecol*.

Escudero, A., Somolinos, R.C., Olano, J.M. and Rubio, A. 1999. Factors controlling the establishment of *Helianthemum squamatum*, an endemic gypsophile of semi-arid Spain. *J. Ecol.*, **87**: 290–302.

Fowler, J. and Cohen, L. 1992. *Practical Statistics for Field Biology*. Chichester, UK: Wiley.

Giess, W. 1971. A preliminary vegetation map of South West Africa. *Dinteria*, **4**: 1–114.

Giess, W. 1981. Die in the zentralen Namib von Südwestafrika/Namibia festgestellten Pflanzenarten und ihre Biotope. *Dinteria*, **15**: 13–72.

Green, J.L., Harte, J. and Ostling, A. 2003. Species richness, endemism and abundance patterns: tests of two fractal models in a serpentine grassland. *Ecol. Lett.*, **6**: 919–928.

Griffin, M. 2000. Annotated checklist of amphibians, reptiles and mammals of the Brandberg, central Namib Desert, Namibia. *Cimbebasia*, **9**: 66–89.

Grubb, P. 2003. Interpreting some outstanding features of the flora and vegetation of Madagascar. *Perspectives Plant Ecol. Evol. Syst.*, **6**: 125–146.

Günster, A. 1992. Aerial seed banks in the central Namib: distribution of serotinous plants in relation to climate and habitat. *J. Biogeogr.*, **19**: 563–572.

Hachfeld, B. 2000. Rain, fog and species richness in the Central Namib Desert in the exceptional rainy season of 1999/2000. *Dinteria*, **26**: 113–146.

Hachfeld, B. and Jürgens, N. 2000. Climate patterns and their impact on the vegetation in a fog driven desert: the Central Namib Desert in Namibia. *Phytocoenologia*, **30**: 567–589.

Harrison, S., Viers, J.H. and Quinn, J.F. 2000. Climatic and spatial patterns of diversity in the serpentine plants of California. *Diversity and Distributions*, **6**: 153–162.

Hedberg, O. 1986. Origins of the afroalpine flora. In *High Altitude Tropical Biogeography* (F. Vuilleumier and M. Monasterio, eds.), pp. 443–468. Oxford: Oxford University Press.

Hickerson, L.L. and Wolf, P.G. 1998. Population genetic structure of *Arctomecon californica* Torrey & Fremon (Papaveraceae) in fragmented and unfragmented habitats. *Plant Species Biol.*, **13**: 21–33.

Ihlenfeldt, H.D. 1994. Diversification in an arid world – the Mesembryanthemaceae. *Annu. Rev. Ecol. Syst.*, **25**: 521–546.

Irish, J. 1994. The biomes of Namibia, as determined by objective categorisation. *Navorsinge van die Nasionale Museum Bloemfontein*, **10**: 549–592.

Jürgens, N. and Niebel, A. 1994. Ecological and floristic peculiarities of lichen fields of the southern Namib. *Mitt. Inst. Allg. Bot. Hamburg* (*Feddes Repertorium*, 1994).

Jürgens, N., Burke, A., Seely, M.K. and Jacobsen, K. 1997. Desert. In *Vegetation of Southern Africa* (R.M. Cowling, D.M. Richardson and S.M. Pierce, eds.), pp. 189–214. Cambridge: Cambridge University Press.

Kessler, M. 2002. The elevational gradient of Andean plant endemism: varying influences of taxon-specific traits and topography at different taxonomic levels. *J. Biogeogr.*, **29**: 1159–1165.

Klak, C., Reeves, G. and Hedderson, T. 2004. Unmatched tempo of evolution in Southern African semi-desert ice-plants. *Nature*, **427**: 63–65.

Kruckeberg, A.R. and Rabinowitz, D. 1985. Biological aspects of endemism in higher plants. *Annu. Rev. Ecol. Syst.*, **16**: 447–479.

Lancaster, J., Lancaster, N. and Seely, M.K. 1984. Climate of the central Namib Desert. *Madoqua*, **14**: 5–61.

Liebhold, A.M. and Gurevitch, J. 2002. Integrating the statistical analysis of spatial data in ecology. *Ecography*, **25**: 553–557.

Linder, P. 2001. Plant diversity and endemism in sub-Saharan tropical Africa. *J. Biogeogr.*, **28**: 169–182.

Louw, S. 1983. The diversity and daily and seasonal activity of ground-living Tenebrionidae (Coleoptera) in the southern Namib and Kalahari ecosystems. *Cimbebasia*, **7**: 35–56.

Mendelsohn, J., Jarvis, A., Roberts, C. and Robertson, T. 2002. *Atlas of Namibia*. Cape Town: David Philip Publishers.

Midgley, G.F., Hannah, L., Roberts, R., MacDonald, D.J. and Allsopp, J. 2001. Have Pleistocene climatic cycles influenced species richness patterns in the greater Cape Mediterranean Region? *J. Med. Ecol.*, **2**: 137–144.

Midgley, G., Hughes, G., Thuiller, W., Drew, G. and Foden, W. 2005. *Assessment of potential climate change impacts on Namibia's floristic diversity, ecosystem structure and function*. Namibian National Biodiversity Programme, Ministry of Environment and Tourism.

Nagel, J.F. 1962. Fog precipitation measurements of Africa's southwest coast. *Notos*, **11**: 51–60.

Nel, P.S. 1983. *Monitering van die beskikbaarheid, gehalte en benutting van voer op die gruisvlaktes van die Kuisebstudiegebied*. MSc thesis, University of Oranje Freestate, Bloemfontein.

Nott, K. and Savage, M.J. 1985. Variation in seasonal and diurnal leaf water potential of a Namib dune succulent. *Madoqua*, **14**: 177–179.

Poot, P. and Lambers, H. 2003. Are trade-offs in allocation patterns and root morphology related to species abundance? A congeneric comparison between rare and common species in the south-western Australian flora. *J. Ecol.*, **58**: 58–67.

Proches, S., Cowling, R.M. and Mucina, L. 2003. Species-area curves based on relevé data for the Cape Floristic Region. *S. Afr. J. Sci.*, **99**: 474–476.

Robinson, E.R. 1976. *Phytosociology of the Namib Desert Park, South West Africa*. MSc Thesis, University of Natal, Pietermaritzburg.

Robinson, E.R. 1978. Phytogeography of the Namib Desert of South West Africa (Namibia) and its significance to the discussions of the age and uniqueness of this desert. *Palaeoecol. Afr.*, **10**: 67–74.

Robinson, M.D. and Seely, M.K. 1980. Physical and biotic environments of the southern Namib dune ecosystem. *J. Arid Environ.*, **3**: 183–203.

Schmiedel, U. and Jürgens, N. 1999. Community structure on unusual habitat islands: a comparison of quartz field vegetation in the Knersvlakte and Little Karoo of southern Africa's succulent Karoo. *Plant Ecol.*, **142**: 57–69.

Scholz, H. 1972. The soils of the central Namib Desert with special consideration of the soils in the vicinity of Gobabeb. *Madoqua, Ser. II*, **11**: 53–51.

Seely, M.K. 1978. The Namib dune desert: an unusual ecosystem. *J. Arid. Environ.*, **1**: 117–128.

Seely, M.K. 1991. Sand dune communities. In *The Ecology of Desert Communities* (G.A. Polis, ed.), pp. 348–382. Tuscon, AZ: University of Arizona Press.

Sole, C.L., Scholtz, C.H. and Bastos, A.D.S. 2005. Phylogeography of the Namib Desert dung beetles Scarabaeus (Pachysoma) MacLeay (Coleoptera: Scrabaeidae). *J. Biogeogr.*, **32**: 75–84.

ter Braak, C.J.F. and Smilauer, P. 1998. *CANOCO Reference Manual and User's Guide to Canoco for Windows*. Wageningen, The Netherlands: Centre for Biometry.

Theron, G.K., Van Rooyen, N. and Van Rooyen, M.W. 1980. Vegetation of the lower Kuiseb River. *Madoqua*, **11**: 327–345.
van der Pijl, L. 1969. *Principles of Dispersal in Higher Plants*. Berlin: Springer.
van Zinderen Bakker, E.M. and Muller, M. 1987. Pollen studies in the Namib Desert. *Pollen et Spores*, **29**: 185–205.
Walter, H. 1983. *Vegetation of the Earth*. Berlin: Springer.
Walter, H. 1986. The Namib Desert. In *Ecosystems of the World*, Vol. 12B (M. Evenari, I. Noy-Meir and D.W. Goodall, eds.), pp. 245–282. Amsterdam: Elsevier.
Ward, J.D., Seely, M.K. and Lancaster, N. 1983. On the antiquity of the Namib. *S. Afr. J. Sci.*, **79**: 175–183.

APPENDIX

Namib endemics that occur in the central Namib Desert and their main attributes

Plant species	Code	Family	Growth form	Dispersal
Aizoanthemum galenioides (Fenzl ex Sond.) Friedr.	Ag	Aizoaceae	herb	none
Aizoanthemum rehmannii (Schinz) H.E.K. Hartmann	Am	Aizoaceae	herb	water
Aloe asperifolia A. Berger	Aa	Asphodelaceae	leaf-succulent	none
Aloe namibensis Giess	An	Asphodelaceae	leaf-succulent	none
Anticharis ebracteata Schinz	Ae	Scrophulariaceae	herb	none
Arthraerua leubnitziae (Kuntze) Schinz	Al	Amaranthaceae	shrub	wind
Cleome carnosa (Pax) Gilg. and Gilg.-Ben.	Cc	Capparaceae	herb	none
Cleome foliosa Hook. f. var. *namibensis* (Kers) Codd	Cf	Capparaceae	herb	none
Eragrostis pygmaea De Winter	Ep	Poaceae	grass	none
Euphorbia giessii Leach	Eg	Euphorbiaceae	shrub	none
Helichrysum marlothianum O. Hoffm.	Hm	Asteraceae	herb	wind
Hermbstaedtia spathulifolia (Engl.) Baker	Hs	Amaranthaceae	herb	none
Lithops ruschiorum (Dinter and Schwantes) N.E.Br.	Lr	Mesembryanthemaceae	dwarf stem-succulent	water
Raphionacme haeneliae Venter and Verheoven	Rh	Apocynaceae	geophyte	wind
Senecio engleranus O. Hoffm.	Se	Asteraceae	herb	wind
Stipagrostis hermannii (Mez) De Winter	Sh	Poaceae	grass	wind
Stipagrostis namibensis De Winter	Sn	Poaceae	grass	wind
Stipagrostis sabulicola (Pilg.) De Winter	Sa	Poaceae	grass	wind
Stipagrostis seelyae De Winter	Ss	Poaceae	grass	wind
Trianthema hereroensis Schinz	Th	Aizoaceae	leaf-succulent	water
Zygophyllum stapffii Schinz	Zs	Zygophyllaceae	leaf-succulent	wind