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# Endemism in Namibia: patterns, processes and predictions

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Sandwiched between the Namib and Kalahari Deserts of southwestern Africa are the karoooid and escarpment biotopes of Namibia which are rich in endemics of many taxa. Most plant, invertebrate, amphibian, reptile, mammal and bird species endemic to Namibia are found in a zone running through, and to the west of, Namibia's escarpment region. There is also an important region of endemism for succulent plants, reptiles and invertebrates in the Succulent Karoo biome. Congruence between endemism hotspots, particularly on rocky substrates, is remarkably high for most taxa, implying broadly similar speciation processes. Possible speciation mechanisms in different parts of the country include the spatial isolation of rupicolous taxa such as insects and reptiles by the formation of large coastal dune fields; the expansion and contraction of wooded savannas during pluvial and interpluvial periods; and global temperature shifts which created highland refugia for frost-susceptible plants and poikilotherms. Areas of endemism and species richness overlap poorly for Namibia's mainly arid-dwelling endemic vertebrates, as richness is highest in the mesic wetlands and woodlands of northeast Namibia. The overlap for succulent plants, insects and arachnids, however, is relatively high. Centres of endemism for plants and vertebrates fall mainly outside protected areas, as few parks were established with biodiversity indices in mind. Our analysis of endemism congruence provides a strong platform for the promulgation of new protected areas to safeguard Namibia's unique biota. Furthermore, analysis of speciation patterns and processes is a useful predictive tool for the identification of other biotically important sites.

*Keywords:* centres of endemism; Namib Desert; species richness; speciation.

## Introduction

The analysis of patterns of endemism and species richness in southern Africa is a daunting task, given the enormity of riches that the region offers. For example, almost 10% of the world's flora occurs in southern Africa (Cowling and Hilton-Taylor, 1984), 30% of the world's fishmoths (Lepismatidae) are endemic to the region (Irish, 1994), more tortoises occur in southern Africa than anywhere else (Branch *et al.*, 1995), and 93% of all geckos are found nowhere else (Bauer, 1993). Namibia also supports the greatest richness of solifugae in the world (R.E. Griffin, this issue). Crowe (1990) and Bibby *et al.* (1992) found that hotspots of endemism for African birds, mammals and amphibians overlap in West African rainforest, the East African Rift Valley and the southwest arid zone of Namibia and South Africa. Analysis of species unique to Namibia is therefore not only essential in national and regional contexts, but also for continental and global perspectives on biodiversity. Part of this process, highlighting areas rich in endemics and looking for congruence among taxa, is crucial for conservation prioritization both inside and outside Namibia. Moreover, congruence of endemism in different taxa can shed light on the

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mechanisms of speciation in this arid zone. This allows predictions about (i) priority areas in which to search for endemics new to science (recently averaging one new reptile per year in Namibia), (ii) where original founder populations of such species may occur, and, by reference to the protected area network, (iii) how effectively this unique diversity is conserved in Namibia.

This paper brings together data on endemic and near-endemic plants, insects, arachnids, amphibians, freshwater fish, reptiles, mammals and birds to answer the following four questions. (i) Are endemics in different taxa clustered in certain congruence zones of Namibia? (ii) Do patterns of endemism suggest waves of speciation that could have resulted from known climatic changes? (iii) Is there a geographical correlation between endemism and species richness? (iv) Are such areas adequately protected in conservation areas? We further investigate whether speciation patterns allow us to predict where other centres of endemism might occur. Specific data on each of the taxa included here can be found in other papers in this special issue (see Robertson *et al.*; M. Griffin; Maggs *et al.*; R. E. Griffin) and in an entomological paper in preparation by E. Marais and J. Irish. Our focus is on reaching broad preliminary conclusions from patterns emerging from across taxa in Namibia.

## Methods

Broad-scale analyses of biodiversity patterns in such a richly endowed region must contend with methodological constraints. First, the operational definition of endemism varies between taxonomic disciplines in Namibia. Second, data accuracy and completeness vary substantially between taxa. For example, only about 24% of all spiders occurring in Namibia, and about 18% of the estimated 35 000 insect species, are described. At the other extreme, the Southern African Bird Atlas (Harrison *et al.*, 1997), comprehensively summarises the distributions of all southern African species and has allowed micro-distribution analysis of Namibia's near-endemics (Robertson *et al.*, 1995; Jarvis and Robertson, 1997). Information quality for all other taxa falls between these two extremes.

In this paper, we define endemic species as do Namibian specialists in each field. Frogs, reptiles and mammals are classed as endemic if 75% or more of the species' total range occurs in Namibia. For birds the limit is set at 90%. For insects, arachnids, flowering plants and freshwater fish, endemism is defined strictly as 100%. In all cases except fish, many of the endemics are arid-tolerant residents of the Namib Desert or escarpment zone. Since this ancient desert stretches marginally into both southwest Angola and northwest South Africa, political boundaries dissect otherwise well-defined ecological boundaries, and Namib Desert endemics are not necessarily completely contained within Namibia. We also note that due to political instability in Angola, the Namibian near-endemics that do occur there are essentially unprotected, so that Namibia must assume the primary mantle of responsibility for their conservation. We thus take this broader definition of 'Namibian endemics' for two reasons: (i) it includes species that might remain unprotected elsewhere, and (ii) if all countries strictly conserved only country-specific endemics, many cross-boundary species would remain unprotected whatever the conservation abilities of their host countries. We thus aim to help prevent numerous species falling through the cracks of narrow, nationally-bound biodiversity conservation programmes in the absence of an effective regional programme. The proportions of endemics stated in this paper are probably conservative estimates, as many as-yet undescribed taxa (particularly insects and

arachnids) probably occur as small, isolated populations which are likely to be endemic. Maps presented here are based on species richness patterns of endemism.

To describe the degree of congruence in endemism for all five taxa for which we have appropriate data (plants, amphibians, reptiles, mammals and birds), we first expressed the importance of each quarter-degree square (QDS) for individual taxa as the proportion of endemics in QDS  $i$ , relative to the total number of endemic species known (i.e. if 68 of 683 endemic plants known occur in QDS  $i$ , it is assigned a value of  $68/683 = 10\%$ ). Proportions for each taxon are similarly computed and summed for QDS  $i$  as a single proportion. The maximum theoretical value is 500% if all five taxa had every endemic species present in square  $i$ . To ensure evenness in this total proportion, we intended to multiply the total proportion for QDS  $i$  by the fraction of taxa represented therein. Hence if QDS  $i$  had a total proportion of 200% but only two of the five taxa occurred there (i.e. it was rich in endemic birds and mammals but no other taxa), the proportion would be reduced to  $2/5$  of 200%, or 80%. However, data inspection showed this to be unnecessary, as the five taxa share very similar distribution patterns across western Namibia. The resulting map gives a more even picture of taxon-rich hotspots. To reduce collecting bias in the maps produced for plant richness, we have presented data in half-degree squares (HDS,  $60 \times 60$  km), rather than QDS. This reduces bias where plants are likely to occur in regions adjacent to frequently collected areas, and is known to reduce bias in the best known data set, birds (Robertson *et al.*, this issue).

For some taxa (birds, mammals, frogs) we are confident that sampling has been sufficient to reveal most or all endemic species. Other taxa, which are unevenly sampled or include cryptic species, may reveal additional endemics with more sampling and genetic analysis. In reptiles, for example, field coverage is good, but genetic work is revealing cryptic species (Gordon and Griffin, 1989). Even with birds we cannot be complacent, as recent genetic work on the arid-zone larks (Alaudidae) in the winter-rainfall area of Namibia has promoted a subspecies of the dune lark *Certhilauda erythroclamys* to a new species, *C. barlowi* based on a genetic divergence of about 2% and an inferred speciation date of about 1 million years (P. Ryan, pers. comm.). Much of the country's terrain is rugged, arid and remote, so more endemics will certainly come to light in the future.

## Results and discussion

### *Endemicity*

The degree of endemism for plants, invertebrates, reptiles (mainly lizards) and frogs is relatively high (Table 1), whereas mammals, birds and fish exhibit levels of endemism below 10%. Fish are a special case as their main habitats are the perennial rivers bordering Angola and South Africa, so even species endemic to these rivers are by definition not Namibian endemics. This is exemplified by the Orange River, where 42% of the 15 species are endemic to the river but not to Namibia alone (Hay *et al.*, in press). Fish diversity is treated in detail by Curtis *et al.* (this issue).

Distribution patterns for plants, frogs, reptiles, mammals and birds are shown in Fig. 1. Each shows a pattern of distribution closely associated with the Namib and Karoo Biomes. Further sampling on mountains, especially inselbergs, will almost certainly reveal more species of insects, arachnids, reptiles, and possibly plants and frogs. In this case the geographic patterns of endemism (Fig. 1) are probably not biased, but the total number of species is certainly underestimated for invertebrates. The same may apply to flowering

**Table 1.** Numbers and proportions of known endemic and near-endemic taxa found in Namibia<sup>a</sup>

	Endemics	All species	Endemism (%)
Fungi	Unknown <sup>b</sup>	Unknown	—
Plants	683	4334	17
Insects	1541	6331 <sup>c</sup>	24
Arachnids	164	1331 <sup>d</sup>	12
Frogs	6	51 ± 5	12
Fish	3	113	3
Reptiles	59	250	24
Mammals	14	200 <sup>e</sup>	7
Birds	14	644	2

<sup>a</sup> Figures are based on studied taxa, which, in some cases, represent less than 20% of the expected total. Endemism levels are therefore conservative estimates.

<sup>b</sup> As fungi are often specific to endemic host species, numerous endemic fungi are expected (Mannheimer and Jacobson, 1997).

<sup>c</sup> This figure represents about 18% of the expected 35 000 insect species in Namibia (E. Marais).

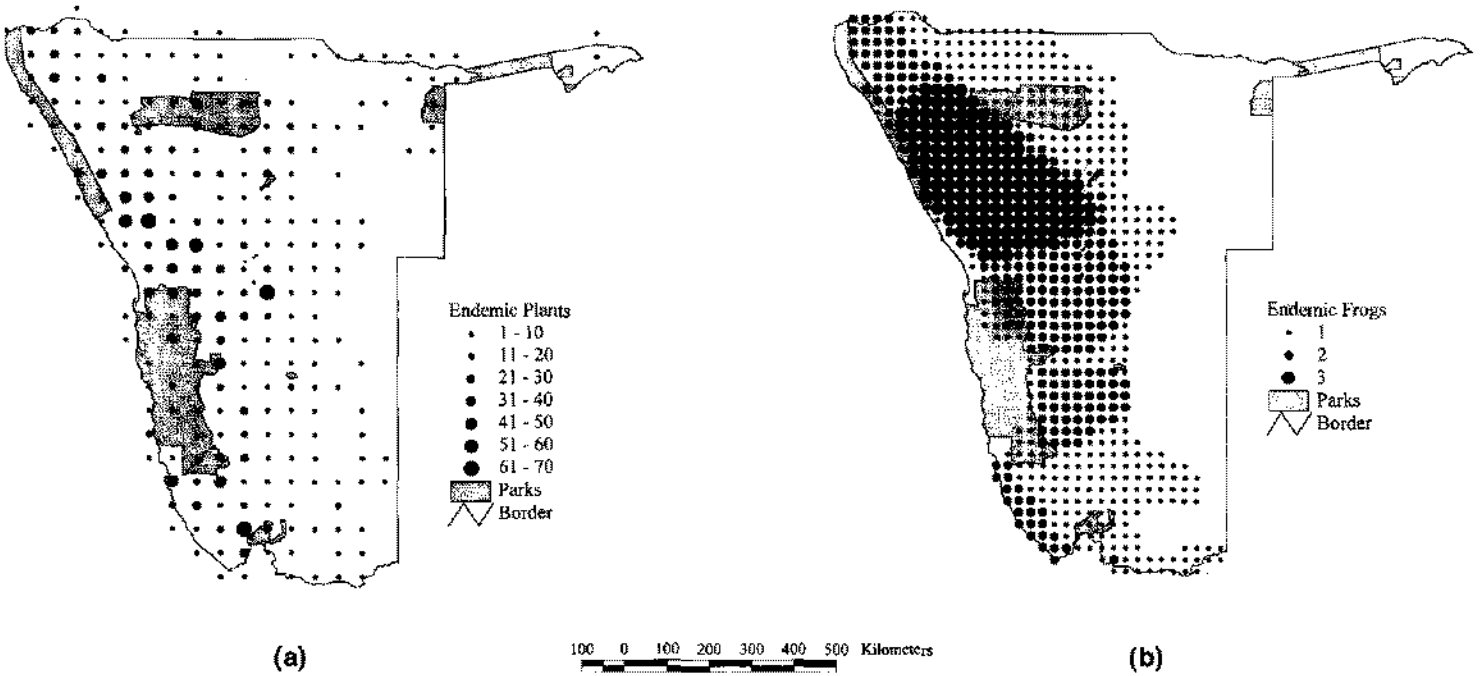
<sup>d</sup> This figure represents about 24% of the expected 5650 arachnids (Scorpions, spiders and allies), in Namibia. Mites are little known and endemism will increase with further study (R. E. Griffin, this issue).

<sup>e</sup> Only terrestrial mammals; excludes 40 marine mammals in Namibian waters (M. Griffin, this issue).

plant species in Namibia, as many are associated with montane areas, where higher rainfall and protection from adverse desert conditions and grazing may promote speciation in isolated populations (Cowling and Hilton-Taylor, 1994). Specialization in such environments may increase where substrates foster the survival of certain varieties of mineral-tolerant plants (P. Craven, pers. comm.), and special adaptations have arisen to tap the limited moisture sources, such as fog, on Namibia's coast, or to attract specific pollinators.

### *Patterns of endemism*

*Invertebrates.* Given that invertebrates form the vast majority of species and biomass (Groombridge, 1992) it is not surprising that less than a quarter of Namibia's insect and arachnid species are described, despite a programme of description and categorization at the National Museum of Namibia dating from 1968. Even so, we can make preliminary estimates of both levels and geographic patterns of endemism (see also R.E. Griffin, this issue). Namibia is highly speciose, with about 35% of the roughly 100 000 southern African insect species occurring within its borders. From the subsample of 6331 recorded insect species, we know that at least 1541 (24%) are endemic, with a high concentration occurring in western Namibia along the escarpment and in the Namib gravel plains (E. Marais and J. Irish, in preparation). Many of these endemic insects are plesiomorphs, that is, phylogenetic relicts isolated for millennia following climate change (Endrödy-Younga, 1982a). If each genus contains only a few species, a long history of residence and isolation can be inferred. Plesiomorphs are commonly found in Namibia's escarpment region (Holm, 1990). Such regions with phylogenetic relicts are often characterized by high endemism and relatively low species richness, whereas regions with a history of oscillating climatic conditions, favouring speciation, feature many endemics and higher overall



**Figure 1.** Patterns of endemism in Namibian plants, mammals, reptiles, frogs and birds in relation to protected areas. Each map shows the species richness distribution of endemics in each taxa for: (a) plants; (b) frogs; (c) reptiles; (d) mammals; and (e) birds. Note that plants are given on a half degree-square basis to reduce observer bias, while all other taxa are shown using quarter-degree squares. The last map (f) indicates the association with highland topography in Namibia and each map shows the country's protected areas. Insects and arachnids could not be shown because mapping is incomplete.

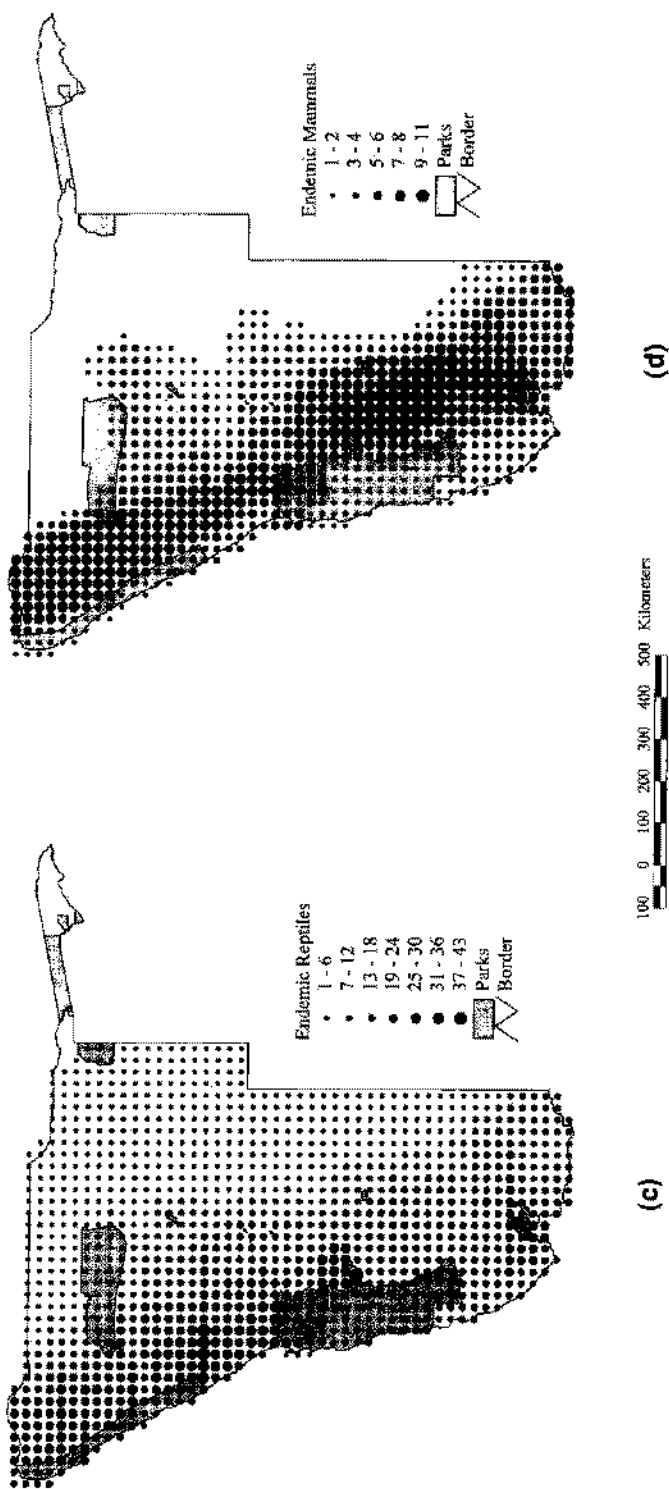


Figure 1. (Continued)

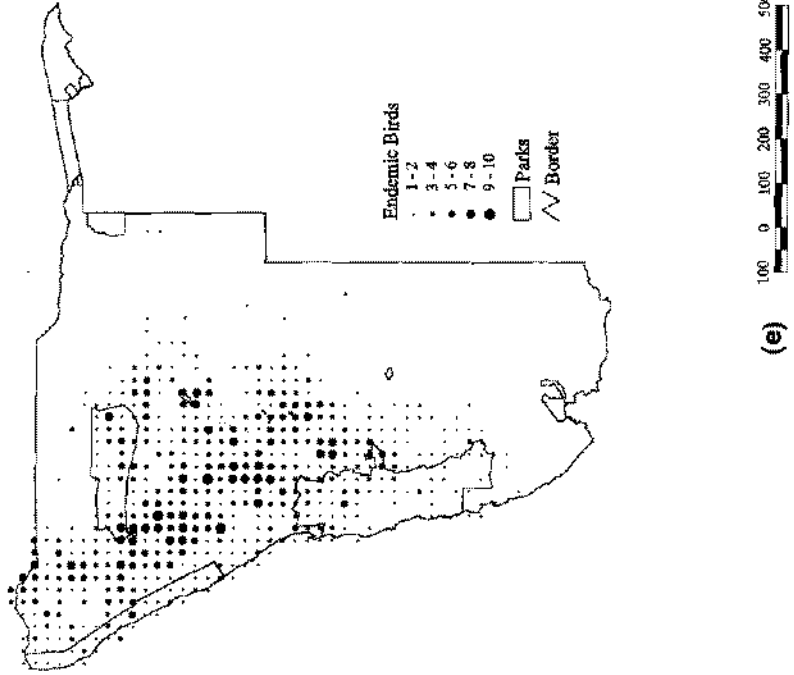


Figure 1. (Continued)



richness (Marais and Irish, in preparation). Both conditions are found along the Namib Desert and surrounding ecotones.

*Plants.* Southern Africa contains almost 10% of the world's flora, concentrated in eight distinct hotspots, defined as the concordance of endemism and high species richness (Cowling and Hilton-Taylor, 1994). Two of these occur mainly in Namibia: the Succulent Karoo biome in the winter rainfall area or 'Sperrgebiet' (forbidden zone) of southwestern Namibia, and the Kaoko region of the far northwest (Cowling and Hilton-Taylor, 1994; Maggs *et al.*, 1994). For example, the well-sampled 2606-m Brandberg massif in the Kaoko region, Namibia's highest mountain, supports 90 Namibian endemic plants and eight of its own (Maggs *et al.*, this issue). Based on present data, endemics are clustered in the Brandberg region; the Hartmann's and Otjihipa Mountains (33 endemics); the Sperrgebiet (62 endemics) which is an extension of South Africa's Richtersveld hotspot; and the Khomas highlands around Windhoek (68 endemics). The Windhoek hotspot may reflect a potential bias arising from uneven sampling effort, as many botanists are based there. However, it also follows the pattern of high-altitude endemism established for other taxa and plants (Fig. 1), since the Khomas highlands around Windhoek contain Namibia's second highest mountain (2479 m) in a transitional arid region (Maggs *et al.*, this issue), representing ideal conditions for speciation in deserts.

*Reptiles and anuran amphibians.* As with plants, endemism in reptiles is related to rocky (rupicolous) habitat in the western deserts. Of the 59 recognized endemic reptiles in Namibia, 83% occur on and around the Brandberg massif, suggesting relict populations (Fig. 1). Another hotspot of 21 endemics occurs in the Sperrgebiet, which includes an unusual rock-dwelling endemic tortoise, the Namba padloper *Homopus bergeri*. Of the six species of Namibian endemic frogs, four occur sympatrically in the escarpment regions of the Brandberg, the Erongo mountains (2350 m) and in the Kamanjab area (Fig. 1). It is likely that others will be discovered in future years, as many species are visible above ground only for short periods when exceptional rains allow reproduction in otherwise harsh environments. Therefore, endemic reptiles and amphibians are found on rocky substrates, with higher mountains supporting the highest species richness. Similar 'mountaintop' patterns of anurans endemic to South Africa have been reported by Drinkrow and Cherry (1995).

*Mammals and birds.* We find a similar pattern of occurrence of rock-dwelling species among Namibia's 14 endemic mammals, comprising mainly bats, rodents and small carnivores. The only large mammal endemic to Namibia is the mountain zebra *Equus zebra hartmanni*, historically found south of the Orange River (Smithers, 1983). About 60% of endemic mammals are rock-dwelling species, and the only ultrapsammophilous species is the Namib dune gerbil *Gerbillurus tytonis* (M. Griffin, 1990). All other endemics occur in escarpment regions, with hotspots in the northern escarpment and especially in the southern regions east of the Namib sand sea (Fig. 1). One of the highest and most isolated points in this southern region is the extinct volcano, Brukkaros (1586 m), where 64% of the 14 endemics potentially occur (Fig. 1); one mammal is endemic to the volcano itself. The distribution suggests relict populations isolated perhaps by low desert temperatures allowing speciation to occur on thermally benign rocky islands. Similar patterns of mammalian endemism are found in the Cape fold mountains of South Africa (Gelderblom and Bronner, 1995).

Finally, for the best known group, birds, ten of the 14 near-endemics in Namibia are escarpment zone species (Fig. 1) whose distribution is defined largely by altitude, most occurring at 600–1200 m (Robertson *et al.*, 1995; Jarvis and Robertson, 1997). Only two of the ten escarpment-zone species are not rupicolous. These are the Rüppell's parrot *Poicephallus ruppelli* and violet woodhoopoe *Phoeniculus damarensis*, which are commonest along the ephemeral rivers in this region (Jarvis and Robertson, 1997) but have a highly restricted range within the catchments of these rivers. Others, such as the rock-runner *Achaetops pycnopygius*, are so rock-specific that vegetation type explains nothing of their distribution (Robertson *et al.*, 1995). Modified Shannon diversity indices are highest where the rivers dissect the escarpment and both riverine and rupicolous groups occur (Robertson *et al.*, this issue). The remaining endemics (larks, korhaan and the Damara tern *Sterna balaenarum*) are found in the dunes, vegetated dunes or gravel plains of the Namib. Only the Cinderella waxbill *Estrilda thomensis*, with a highly restricted range in southern Angola and along the Kunene River, does not fall into the arid zone category (Barnard, 1997).

If we consider endemic birds from a regional perspective, we find that no less than 18% (166) of the approximately 900 southern African bird species are endemic to the arid or semi-arid zones. Of these, 70% (116) can be classified as strictly Southwest Arid Zone endemics, a term which includes South Africa's Karoo Basin (Clancey, 1986; Brown, 1997), although most are not rupicolous. Therefore, like other taxa, most endemic Namibian birds are escarpment-loving species, but are more restricted to northwestern Namibia than other taxa. Both Namibian and southern African endemics are mainly arid-dwelling.

Our conclusion from this summary of endemism across better-known Namibian taxa is that hotspots are closely associated with rocky substrates, especially inselbergs and mountain ranges, for all vertebrates and plants. Insect and arachnid endemism is more closely tied with gravel plains and sand dune movement. All endemics are to some extent associated with arid zones.

*Congruence between species richness and endemism.* Of the taxa so far investigated, only plants and arachnids show an association between richness and endemism. The association for plants holds in southern Africa generally (Rebello, 1994) and Namibia specifically (Maggs *et al.*, 1994). Among arachnids, areas of richness and endemism overlap for solifuges and scorpions, but not for spiders, which are more speciose in mesic regions and show higher endemism in arid regions (R.E. Griffin, this issue). Aquatic and terrestrial insects also show a poor richness-endemism correlation, as richness declines with aridity in terrestrial insects (Marais and Irish, in preparation) and most endemic aquatic insects are associated with specialised desert and karst wetlands (Curtis, 1991; Curtis *et al.*, this issue).

Amphibians show perhaps the most pronounced peak of species richness in the Caprivi wetlands of northeast Namibia, where a mean rainfall of 600 mm year<sup>-1</sup> supports 38 species (M. Griffin, this issue). The same pattern is found to a lesser extent with mammals, which show the highest richness in these wetlands (Griffin and Grobler, 1991). Hence, both taxa show little overlap between areas of high richness and endemism. Reptiles show two regions of high species richness, one in Caprivi where snakes are particularly species rich due to the influence of wetlands, and one in the west where reptiles are associated with rocky habitat. The richness-endemism correlation is thus higher for reptiles because of this overlap in the arid west (M. Griffin, this issue).

For birds, species rich areas are mesic areas harbouring tropical species from central Africa (Fig. 1), such as the Okavango River basin. The Mahango Game Reserve is the major hotspot for avian species richness (see Fig. 1 in Barnard *et al.*, this issue), while the wetlands and floodplains of eastern Caprivi support two thirds of all Namibian bird species (Schlettwein *et al.*, 1991). There is thus no overlap between the mesic high-richness zones and arid high-endemism zones. In an attempt to separate the contribution of wetland and terrestrial birds to avian diversity in northeastern Namibia, diversity indices were calculated separately for these two groups. Robertson *et al.* (this issue) found that species diversity of both terrestrial and wetland birds is high in the Caprivi region, indicating that high diversity cannot be attributed solely to an increase in the wetland bird component.

We conclude that for most water-dependent taxa, there is little or no correlation between species richness and endemism, while for those taxa that have successfully adapted to adverse arid conditions (e.g. succulent plants) or prefer warm rocky substrates and are independent of surface water (arachnids, reptiles) there is relatively strong overlap of richness and endemism. The key ingredient differentiating the two categories thus appears to be water dependence. The lack of correlation between species richness and endemism hotspots is a common phenomenon among many vertebrates in other parts of southern Africa (Siegfried and Brown, 1992; Lombard, 1995a,b) and is also apparent elsewhere (Prendergast *et al.*, 1993). In South Africa, the poor correlation reflects the influence of tropical species increasing species richness values in the northeast of the country, whereas endemism is concentrated in the small but enormously rich Cape Floral Kingdom in the southwestern Cape Province (Siegfried and Lombard, 1996).

### *Evolutionary processes*

*Shifting sands.* As the majority of Namibia's endemics are (i) arid-adapted, (ii) found in the west of the country, and (iii) associated with escarpment, inselberg or dune habitat, we can draw some tentative conclusions regarding processes that led to their evolution. We assume throughout that speciation occurs allopatrically, such as when climatic change shrinks and divides existing populations into small and isolated sub-populations in which genetic change can occur rapidly. Of course this is not the only mode of speciation (Vrba, 1980, 1985; van Valen, 1973), but it is most consistent with present-day distribution patterns. We also note that Namibian ecologists often fall into two camps in their interpretation of speciation processes. Entomologists favour speciation through isolation caused by micro-climatic factors such as extreme aridity (Marais and Irish, in preparation), while vertebrate ecologists tend to favour speciation through larger-scale climatic shifts which inhibit gene flow, through the expansion and contraction of woodlands (e.g. Vrba, 1985; Kingdon, 1990). The two explanations differ in scale, but are not mutually exclusive.

Much of the Namib Desert is a mosaic of dune fields, gravel plains and inselbergs. Many closely related species of arachnids, insects and lizards differ morphologically between coastal gravel plains or rocky areas separated by dune fields (Haacke, 1982; Endrödy-Younga 1982a; E. Griffin, 1990; Irish, 1990; M. Griffin, this issue). These rocky 'islands' have been isolated by a sea of sand, a relatively inhospitable habitat for most species. However, where taxa such as insects, spiders and lizards have specialised in dune habitats, the surrounding rock has become the inhospitable habitat. Clear evidence for this is seen in species found in fast-moving barchan dunes, which can move some 50 m per year

with the dominant southerly winds, taking their fauna with them. Where such dunes have separated from well-defined coastal dune fields, dune-specific endemics are both predicted and found (Endrödy-Younga, 1982b; Irish, 1990). Coastal gravel plains and inselbergs became surrounded and isolated by these shifting sands, providing ideal conditions for speciation in rupicolous taxa, especially flightless species which have reduced opportunities for gene flow back to source populations. In several insect taxa, including tenebrionid beetles, older species occur in the southern Namib and more recent species in the north, taken there by barchan dunes (reviewed by Irish, 1990). Sand-dwelling or psammophilous species frequently evolved from rock-dwelling ancestral ones, as shown for several insect genera (Penrith, 1979; Endrödy-Younga, 1982a; Irish, 1987). The palaeodesert evolved as the southern Atlantic Ocean opened up about 80 My (Ward and Corbett, 1990). It then became more arid when the Benguela Current formed 10 million years. Newly evolving conditions associated with the Benguela, such as coastal fog belts, also promoted speciation and endemism in the post-Gondwana biota.

Does this 'shifting sand' hypothesis, originally proposed for insects, explain patterns of speciation in other Namibian fauna and flora? Some of the strongest evidence comes from *Aporosaura* lizards found in dune habitat either side of extensive gravel plains (Gordon and Griffin, 1989). These gravel plains start in the central coastal regions and end at Terrace Bay, ca 300 km north. Genetic evidence from these sand-diving lizards reveals genetically distinct but morphologically similar populations that diverged about 5.1 million years (Gordon and Griffin, 1989), a period when sea levels dropped and dune fields expanded along coastal regions, later to be divided as sea levels rose again (see Ward and Corbett, 1990). Isolation of populations therefore can be traced to sea level changes about 5 million years (Gordon and Griffin, 1989). As with insects, northerly forms are derived from southerly forms, since sand dune movement is south to north. This scenario is only likely for coastal areas, as large dune fields probably did not extend far inland. What other processes associated with aridity may have isolated populations, especially in montane regions, promoting speciation?

*Rainfall and global temperature change.* At least two other factors, rainfall and temperature, may have influenced speciation processes in Namibia. Interpluvial corridors, dry savannas that spread across south-central Africa, joined east and southwest African faunas (Balinsky, 1962; Kingdon, 1990). These allowed two-way movement of arid-adapted taxa, until wetter periods again promoted continuous mesic woodland, separating savanna-dwelling taxa from parental stock and allowing speciation (Cooke, 1962; Irish, 1987). Supporting evidence for rapid changes in rainfall near the Namib coast within the last millenium is given by Vogel and Rust (1987). This explains some of the insect species groups in southern Africa which clearly have a northern origin (Irish, 1990) and many other insect taxa with disjunct distributions (Marais and Irish, in preparation). It also explains, for example, the disjunct distributions of two bird species, the violet woodhoopoe *Phoeniculus damarensis* and spike-heeled lark *Chersomanes albofasciata* in southwest and east Africa, and mammals such as black backed jackal *Canis mesomelis* and oryx *Oryx gazella* (Kingdon, 1990; Coe and Skinner, 1993). It may also explain the existence of a hunter-gatherer people of Khoi-San descent, which occur as an isolated group in northern Kenya (Pfeiffer, 1977), and nowhere else until Namibia and Botswana.

The second possible mechanism promoting speciation in the desert is global temperature changes associated with consecutive ice ages over the last 60 My and deduced from

deep sea cores (Brain, 1985). For example, between about 20 and 10 million years ago mean temperatures dropped by about 10°C, resulting in a major Antarctic ice cap. Marked oscillations have occurred 17 times over the last 1.7 million years, or approximately once every 100 000 years (Brain, 1985). In southern Africa this explains well the distribution of some plants such as the mopane tree *Colophospermum mopane* whose Namibian distribution is separated by a cool (5°C isotherm) corridor from those in south-central Africa. It also explains the distribution of South African grassland and some of its associated vertebrates (Brain, 1985). For frost-intolerant species such as desert-dwelling poikilotherms, low temperatures could as easily explain their distribution on mountain ranges as does surrounding sand acting as a habitat barrier. This remains to be explored, but could be quickly tested using overlays of minimum temperatures and species' ranges.

While the shifting sand scenario may explain patterns of evolution in insect and reptile faunas, especially gecko speciation within isolated rocky islands (Haacke, 1982; Bauer, 1993), it cannot explain endemism patterns in other Namibian taxa. For birds we do indeed find rock-dwelling, escarpment-clustered endemics (Fig. 1). Many of the distribution patterns of ten endemic bird species are well explained by altitude alone (Robertson *et al.*, 1995; Jarvis and Robertson, 1997). Many also have higher population densities in more northerly escarpment regions (Hall, 1960; Jarvis and Robertson, 1997). However, because these northern highland areas were too far inland to be affected by the predominantly coastal dune fields, the expansion and contraction of woodland and savanna in pluvial and interpluvial periods may be the simplest explanation. Expansions of woodland towards the coast may have isolated the rocky uplands into habitat islands for arid species where speciation was promoted. For frost-intolerant species, oscillations in global temperatures, particularly decreases in minimum temperature, may have broken up the contiguous distribution of some species, leading to speciation. This is more likely if the refugia (highland massifs) act as heat sources or provide physical or thermal shelter within crevices and fissures in the rock.

Another group of avian endemics are clustered in the interdune gravel substrate. These include the Damara tern and Gray's lark *Ammomanes grayi*. Three other southwest arid endemics are strictly sand or dune-dwelling species: Barlow's lark, dune lark, and in South Africa, the red lark *Certhilauda burra*, found exclusively on red Kalahari sands (Dean *et al.*, 1991). These species then may have evolved in habitat islands created when pluvial periods surrounded dune areas with wooded savannas, divided perhaps by ephemeral rivers that once reached the coast (Jacobson *et al.*, 1995). Only Barlow's lark, with a speciation date tentatively put at 1 million years (P. Ryan, pers. comm.), gives any idea of when the most recent processes may have taken place.

#### *Predicting unmapped hotspots of endemism*

We have concentrated on speciation processes because they allow us to make tentative predictions of where other, undescribed endemics may occur, based on the speciation processes thought to have produced the present distributions. Predicted sites for new endemics include large mobile sand dunes, particularly those isolated from major dune fields; isolated gravel plains; large but little-known inselbergs; highland peaks, wetlands and valleys in the Kaoko escarpment and other mountain ranges; and possibly rain shadow pockets within the Succulent Karoo biome. Since Namibia still possesses remote and inaccessible areas where even the most adventurous biologists have not collected, and since many species only reproduce (or indeed appear) in times of high rainfall, such regions

should be targeted for further enrichment of Namibia's list of endemics. Further genetic analysis of potential cryptic species will aid this process.

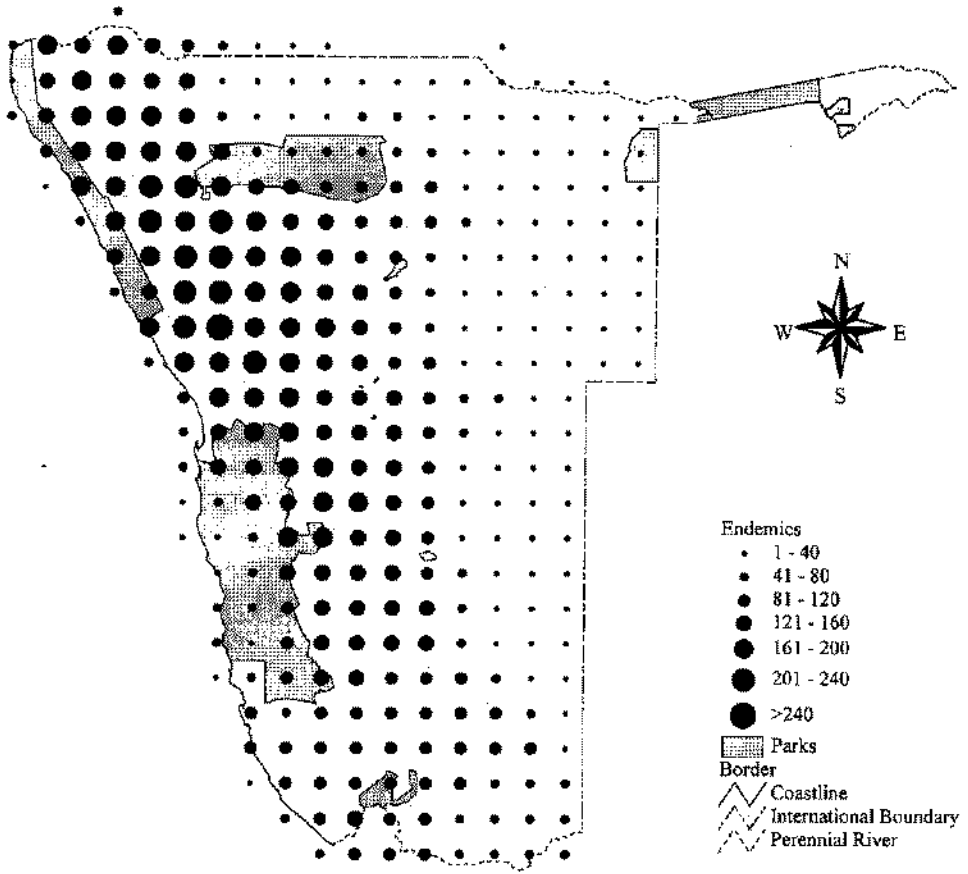
#### *Congruence between endemic taxa and predicted hotspots*

To get a first-order approximation of taxon-rich hotspots of Namibian endemics, as an index of priority conservation sites, distribution patterns in Fig. 1 were amalgamated in one map based on the number of taxa represented in any one QDS (see Methods). The resultant distribution from the five taxa combined (Fig. 2) shows clustering in the Kaoko escarpment, plains and inselbergs of the northwest, particularly at Brandberg; at Brukkaros volcanic crater in the south; and in the winter-rainfall Succulent Karoo biome of the southwest. These areas are the richest endemic regions in Namibia. Importantly, they all fall outside formally protected areas (Fig. 2). Ironically, the Kaoko escarpment was once a major part of 'Game Reserve No. 2', now the Etosha National Park, providing protection for endemics and acting as a corridor for large mammals such as elephant *Loxodonta africana* and lion *Panthera leo* to migrate down ephemeral riverlines to the Skeleton Coast. The Kaoko portion of the reserve was deproclaimed in 1963 for political-ideological reasons (Barnard *et al.*, this issue). By proclaiming the four top endemic-rich areas as protected sites, a large proportion of endemic plants, amphibians, reptiles, mammals and birds would be protected. Considering that the highest population densities of endemic birds occur mainly in the northern regions (Robertson *et al.*, this issue), viable populations of many endemic birds may also occur within such areas. Quantitative analysis is now required to determine the minimum area that would afford protection to all endemic taxa described in this paper. Our analysis identifies the priority hotspots of endemism as a first step toward appropriate conservation area selection.

#### *Where would protected areas best be sited?*

Most of southern Africa's protected areas were chosen either because they contained large ungulates of interest to big game hunters, or because the land was of little use to the government of the day (Brown, 1992; Siegfried and Lombard, 1996; Barnard *et al.*, this issue). Even when these parks did fortuitously cut across regions rich in endemics, some areas were later deproclaimed for dubious political reasons (Schoeman, 1996; Barnard *et al.*, this issue). While conservationists and systematists of the day may not have had access to sophisticated mapping, databases and genetic analyses, they could have provided a fairly accurate intuitive guide to areas rich in species and endemics.

For plants, much of the work on optimal design of protected areas throughout southern Africa is that of Rebelo (1994). This study, which includes all plant species, serves only as a first approximation for Namibia because it relies on limited and somewhat outdated data for Namibia. The pattern of endemism depicted in Fig. 1a is updated from Rebelo's work, but is still far from complete. Rebelo (1994) found through an iterative selection process that 22% of the land of southern Africa is required to include all flora in protected areas. However, half the taxa can be protected in just 0.4% of the land area (mainly the Cape Floral Kingdom) and 10% of the land area can preserve 93% of all taxa. For Namibia, the important points to emerge from this analysis were that the Succulent Karoo and Kaoko escarpment are badly in need of protection. The total number of QDS units (ca 30 × 30 km) required to protect all southern African plants within just one QDS is 145 additional squares over and above the 13.6% of the land area then protected by the Namibian government. Since about five of these squares identified by Rebelo were in fact



100 0 100 200 300 400 500 Kilometers



already inside protected areas, the number required is about 140 extra QDS. This represents an additional 11.1% of the land area of Namibia, slightly less than the additional protection required in South Africa (13%). Note that this analysis is for all plant species in southern Africa, and the required area may be less for endemic species within Namibia. Barnard *et al.* (this issue) discusses the highly skewed representation of biomes and vegetation types in formal and informal protected areas within Namibia.

In summary, the near-endemic plants, terrestrial insects and arachnids, amphibians, reptiles, mammals and birds of Namibia are predominantly arid-adapted, confined either to the rocky escarpment or to the dune fields and gravel plains of the Namib Desert. The mobility of sand on the coastal plains provides the best explanation of speciation: rocky habitats became isolated islands in mobile sand seas, promoting speciation. Oscillating patterns of regional rainfall and global temperature may have isolated species on rocky islands and inselbergs further inland through intolerance to low temperatures. The arid habitat of Namibia's endemics means that in many cases there is no overlap between species richness and endemism hotspots, since richness is associated with mesic and wetland habitats for most taxa. For taxa independent of surface water, however, this overlap is high. There is strong congruence in the distribution patterns of endemic plants and animals in western Namibia, and four regions (the Kaoko escarpment, the Sperrgebiet or Succulent Karoo, the extinct volcanic crater Brukkaros, and the Brandberg massif) are top priority areas for urgent biodiversity protection measures. Namibia's endemic species are inadequately known, and intensified field and genetic sampling in habitats predicted to contain undescribed endemic species, particularly during high rainfall events, will certainly add to the country's list of endemic species.

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**Figure 2.** Hotspots of endemism for five taxa in Namibia. The map is an amalgamation of endemism in plants, reptiles, amphibians, birds and mammals in Namibia (Fig. 1), with proportions for each taxon plotted and summed across all taxa per half-degree square. The richest squares represent those that possess the greatest proportion of endemic biota in Namibia, and are thus conservation priorities. Note the clustering in the highland region centred on the Brandberg inselberg, Namibia's highest mountain.



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