CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

Chapter Outline

A. Diversity and Endemism

Southern Africa has a diverse moss flora with strong tropical African affinities. Moss species are not uniformly distributed throughout the region but are concentrated in the shape of a horseshoe along and below the Great Escarpment. Diversity is greatest in the mountains of the south-western Cape, KwaZulu-Natal, and Mpumalanga/Northern Province. In the FSA area moss species richness increases with altitude to peak between 500 m and 1000 m, above which species numbers gradually decrease. Along the eastern escarpment of southern Africa species numbers peak in the montane forest belt (1001 m – 1500 m).

As a result of this study the numbers of species and endemics in each southern African moss family and genus, the largest families and genera, the most frequently collected mosses, and the most widely distributed species, could be identified. Lists of endemics, aquatics, and mosses with recent range expansions are provided for the first time.

Moss endemism is most pronounced in the south-western Cape, and in particular on Table Mountain. In keeping with results from other parts of the world, endemism is significantly lower in the mosses than the vascular plants of the region at all taxonomic levels.

The main centres of moss diversity and endemism overlap in southern Africa to form 'hot-spots', which largely coincide with the 'hot-spots' described for vascular plants. Although collecting bias is responsible for concentrations of species and endemics in many areas, moss diversity and endemism were found to be strongly correlated with habitat heterogeneity and mean annual rainfall. The more diverse the habitat and the higher the rainfall, the more species as well as endemics are present. This is in agreement with existing hypotheses of a broad-scale correlation between environmental heterogeneity and climate on the one side, and vascular plant diversity and distributions on the other.

B. Numerical Analysis

Attempts to analyse bryophyte distributions using large data sets have been limited and this is the first such study in Africa. It also is the first broad-scale, numerical analysis of plant distributions in the Flora of Southern Africa area.

Although the data sets used in the analyses are rather 'noisy', intended for mapping species distributions rather than numerical analysis of distribution patterns, the results of the TWINSPAN classification and DECORANA ordination show that the numerical methods used in this study have been remarkably successful in delimiting broad-scale phytogeographic patterns in the moss flora of southern Africa.

After deleting species poor grid squares from the complete data set, TWINSPAN successfully divided the grid squares, as well as the moss species, into two major groups. The main groups were subdivided into two groups each (2nd level of division), which in turn were subdivided to give eight groups at the 3rd level of division. Most of the groups delimited by the TWINSPAN classifications are coherent and ecologically interpretable.

The DECORANA ordination programme has successfully revealed broad-scale compositional as well as distributional gradients in the moss flora which could be related to major climatic gradients in the study area.

C. Bryogeographic Regions

The numerical classification of grid squares divided the study area into two main regions: 1) a temperate or austral region in the central and western parts of southern Africa, and 2) a subtropical or palaeotropical region in the northern, eastern and southern parts of southern Africa. The temperate region has a xerophytic moss flora while the flora of the subtropical region is mesophytic. Pleurocarpous mosses make up an increasingly larger proportion of the moss flora as one moves from temperate areas in the west to subtropical areas in the east and south of the study area. Results of the numerical analysis indicate that the boundary between the two main floristic regions in southern Africa is located much further to the north than generally accepted.

The temperate region is subdivided into the Karoo-Namib and Highlands Regions, and the subtropical region into the Zambezian and Afromontane (including the former 'Cape') Regions. The four Regions are further subdivided into eight Domains. The Afromontane Region is not only the largest bryofloristic region in southern Africa, it also boasts the largest moss flora, and most of the centres of moss diversity and endmism are located in this phytochorion.

Although there is a high degree of congruence between the bryofloristic regions and the floristic regions recognised in contemporary vascular plant classifications (Werger 1978, White 1983, Goldblatt 1978, Cowling & Hilton-Taylor 1997), I would like to point out a number of important differences between the two:

- The Afromontane Region is not part of the temperate, but the palaeotropical regions of Africa.
- A separate 'Cape' phytochorion is here only recognised at the level of domain, and then as a subdivision of the Afromontane Region. This supports the hypothesis by Linder (1990) that the 'Cape' phytochorion forms part of the Afromontane Region, but not in a combined 'Afrotemperate Region' as suggested by him. The combined Afromontane Region is formally described for the first time in this study.
- A separate Tongaland-Pondoland Region is not recognised in the bryogeographic scheme.
- Although it is generally accepted that the Karoo-Namib Region is of palaeotropic affinity (Werger 1978, Hilton-Taylor 1994), this study clearly shows that it is part of the temperate region of southern Africa.
- The bryofloristic Highlands Region is restricted to high altitude areas of southern Africa and does not occupy the sandy Kalahari basin.
- The Afro-alpine flora of Lesotho is not part of, or closely related to the Afromontane flora. The bryogeographic classification shows that it belongs to the temperate flora of the Highlands Region.

Rutherford & Westfall (1986) argue that if phytochoria were classified objectively (according to rigorous phytosociological methology), based on adequate sampling, then correspondence to biomes would be better. Hilton-Taylor (1987) supported this argument based on "Preliminary indications from my analysis of floristic data...". However, Rutherford (1997) has recently stressed that due to different criteria used in the determination of biomes and phytochoria, they do not necessarily coincide. In a comparison of floristic and structural vegetation classifications of the same island, Lux & Bemmerlein-Lux (1998) recently found that "...structural vegetation units reflect a short-term development." while "...the floristic units reflect the sum of the effective environmental factors over the course of time,...". Although there is considerable congruence between the numerically determined bryofloristic Regions of this study and the Biomes of Rutherford & Westfall (1986), there is no obvious improvement from conventional phytogeographic schemes, which indicates that there might indeed be significant differences between structural and floristic classifications in the flora of southern Africa area.

D. Bryogeographic Elements

The mosses of southern Africa are divided into two main floristic elements: 1) a xerophytic element mainly distributed in the winter rainfall and semi-arid, temperate areas of southern Africa, and 2) a mesophytic element distributed in more stable, subtropical habitats of the northern, eastern and southern parts of southern Africa. The xerophytic element is dominated by acrocarpous mosses (inluding the ephemerals) while the mesophytic element contains most of the pleurocarpous mosses.

The xerophytic element is subdivided into the Eastern Highlands and Cape Elements while the mesophytic element consists of the Afromontane Grassland and Afromontane Forest Elements. The Elements are subdivided into eight Subelements. The Afromontane Forest Element is by far the largest of the elements and contains the most FSA endemics. Many of the distribution centres in the bryogeographic elements are known phytogeographic centres of the vascular plants.

The majority of bryogeographic Elements are distributed in the Afromontane Region while the greatest number of Subelements displays a Cape bias. This stresses the phytogeographic importance of the Afromontane islands in the south-western Cape, especially the Table Mountain locality.

E. Indirect Gradient Analyses

The DCA ordination revealed a main longitudinal (east–west), and secondary latitudinal (north south) and altitudinal gradients in the floristic composition of the grid squares as well as the geographic distribution of the species. The main east–west gradient in the moss data coincides with the main east–west climatic gradient in southern Africa, best explained by moisture parameters, in particular mean annual rainfall. The secondary gradient in the data, running latitudinallly as well as altitudinallly, appears to be related to temperature, and in particular the effect of temperature on the availability of moisture.

The fact that the DCA ordination revealed broad-scale compositional and distributional gradients in the data indicates that fine-scale heterogeneity in the study area has been averaged out by the coarseness of the grain (the grid size) as well as the deletion of species-poor grids from the complete data set. The variation may therefore be explained satisfactory at the hand of a few major climatic variables, in this case rainfall and temperature, which is in line with hypotheses proposed for vascular plants in southern Africa.

F. Needs and Prospects for Future Research

In my opinion the following paradigms retarded progress in southern African phytogeography in the latter part of the Twentieth Century:

1. The pre-occupation with the Cape flora (Cape Floristic Kingdom), or as Nordenstam (1969) put it, the "Tendency to particularize the Cape Flora.".

2. The introduction and indiscriminant application of non-hierarchical categories, in particular the 'centres of endemism', in the classification of geographic areas (floristic regions).

3. Confusion between, and the misapplication of the two main concepts in floristic plant geography, i.e. phytogeographic (floristic) regions and phytogeographic (floristic) elements.

4. The lack of clear and precise definitions of phytogeographic terms currently used in southern African studies.

5. The use of endemic or 'ecologically important' taxa only in the delimitation of floristic regions.

6. The currently recognised centres of vascular plant diversity and endemism (hot-spots) in southern Africa as a mixture of floristic regions, biomes, geological formations, and distribution centres of high diversity and endemism.

7. The lack of a broad-scale, subcontinental classification of floristic elements based on the distribution of all the plants in southern Africa.

I would now like to propose the following guide-lines for future phytogeographic studies in southern Africa:

Guide-lines for future phytogeographic studies in southern Africa

1. Phytogeographic analyses should in future be based on distribution data of as many taxa as possible, preferably all plants present in the study area. At the regional or subcontinental scale such a database already exists in the form of PRECIS (Magill *et al.* 1983), which contains the distributions of all southern African flowering plants, ferns, and bryophytes represented in the National Herbarium, Pretoria.

2. A clear distinction should be drawn, right from the start, between the the two main concepts in floristic plant geography, i.e. floristic regions and floristic elements.

3. Repeatable (more or less objective), numerical techniques should be employed to identify patterns in the distribution data, and to relate these patterns to environmental variables.

4. The term 'centre' should rather be used to describe concentrations of species (or higher taxa) within the distribution areas of floristic elements or floras, and not to describe floristic regions.

5. It is confusing to group different categories of species and endemic-rich areas together as centres of species diversity and endemism without explaining how they differ and how they came about. The challenge is now to identify and describe centres of plant diversity and endemism in southern Africa in a uniform and objective way.

6. Although centres of diversity and endemism generally overlap in southern Africa to form 'hot-spots' (Cowling & Hilton-Taylor 1997), this is not necessarily always the case. The two kinds of centres should therefore be determined separately and then compared.

7. The grain of the study (the area of recording, e.g. the degree grid square system) should be set as fine as possible in order to lay down boundaries with some accuracy. This in turn will enable ecologists, environmentalists, conservationists etc. to make more use of phytogeographic maps in regional studies.

Visual comparison between maps is a rather unsatisfactory, although not necessarily an ineffective method of interpreting the ordination results. A more objective, direct gradient analysis approach, as performed by canonical correspondence analysis (CCA), should prove to be a most worthwile and pertinent next step in the bryogeographic analysis of the distribution data. However, a limiting factor in such an analysis is the lack of detailed environmental (climatic) data for large parts of South Africa and neighbouring states (O'Brien 1993, Schulze & Kunz 1995).

The all important first steps of identifying and describing bryogeographic regions and elements in southern Africa have now been taken. The patterns identified here are not only due to similarities among areas in their environmental parameters, or similarities among species in their ecological tolerances, but also to the evolutionary histories of areas and species. Historical reasons for the observed bryogeographic patterns might now be sought within the broad climatic parameters laid down in this study. Such explanations should, however, not overstep the ecological requirements of the taxa. As Cowling *et al.* (1997b) aptly put it: "A new synthesis is emerging where ecological and historical explanations are not seen as contending assertions, but as integrated parts of realistic and general explanations of ecological diversity."