Contributions of N H Speck to the biogeography of Proteaceae in Western Australia

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Abstract

When considering the study of the biogeography of the Western Australian flora, botanists such as Diels, Gardner and Beard spring to mind, but what has not been generally recognised outside of Western Australia was the substantial contribution of Dr Nathaniel Speck. Speck was the first to quantify patterns of species richness for the Proteaceae in south-western Australia. In addition he provided detailed community mapping of the Swan Coastal Plain in particular, and of the south west in general. Speck was also the first to propose that the Mt Lesueur region (one of the two major centres of biodiversity in Western Australia) should be recognised as a separate botanical district.

The biogeographic patterns of the Proteaceae reported by Speck are compared here to a recent synthesis based on over 21000 collections held in the Western Australian Herbarium. The current analysis was largely consistent with the Speck's 1958 work, except that the gradients in species richness away from the two major centres of species richness are less steep than previously described. This strong correlation between the two studies is despite a taxonomy that recognises more than twice the number of taxa that he dealt with and availability of many more collections across the south west.

A brief outline of Speck's botanical and ecological work and a bibliography of his published and unpublished work are included.

Introduction

The diversity and richness of the Western Australian flora have long been recognised (Diels 1906; Gardner 1944; Hopper 1979), as has the biogeographical patterning of the flora (Diels 1906; Speck 1958; Beard 1980, 1990). While the names of Diels, Gardner and Beard are readily recognised, the contribution of Nathaniel Henry Speck has often been overlooked outside of Western Australia. Speck mapped the vegetation pattern on the Swan Coastal Plain in the early 1950s and he later extended this across the whole of the southwest (Speck 1958). Based on this work he proposed that the Lesueur region should be recognised as a separate botanical district. Beard's (1980, 1990) phytogeographic mapping did not accept this division, but recent work on the biogeography of the genus *Banksia* has strongly argued for the resurrection of this district (Lamont & Connell 1996).

The detailed biogeographic patterning of many of the major genera and families is now well documented across the south-west of Western Australia (Speck 1958; Hopper & Maslin 1978; Hopper 1979; Taylor & Hopper 1988; George 1991; Keighery 1996; Lamont & Connell 1996). Speck's (1958) analysis of the biogeography of the Proteaceae was the first study to quantify these patterns. It is now almost 40 years since this ground-breaking work was published, and here we compare the results of his 1958 study with our present understanding of biogeography of the Proteaceae based on collections held in Western Australian Herbarium.

Methods

Speck (1958) mapped 426 taxa of the Proteaceae across the southwest on a 50000 yard (28 mile) grid, and distribution patterns were analysed on both a genus and family basis. A comparable recent analysis was compiled from distribution data for 882 taxa (in 17 genera and 779 species) based on collections held in the Western Australian Herbarium. Over 24000 collections of Proteaceae are held in the herbarium and in excess of 21000 have geographic coordinates that could be used in this analysis. Distribution patterns were determined on a one degree latitude and longitude grid basis across the State. This grid was both larger and more extensive than that used by Speck (1958). Analyses were undertaken for all taxa and for *Grevillea, Lambertia* and *Adenanthos*. These were compared with Speck's (1958) earlier analysis.

Results and Discussion

Comparison of biogeographic patterns

Speck's (1958) analysis of the 426 taxa of Proteaceae showed two centres of species richness, one on the northern sandplain centred on the Mt Lesueur area and a second on the south coast stretching from the Stirling Range to the Fitzgerald River area (Fig 1).

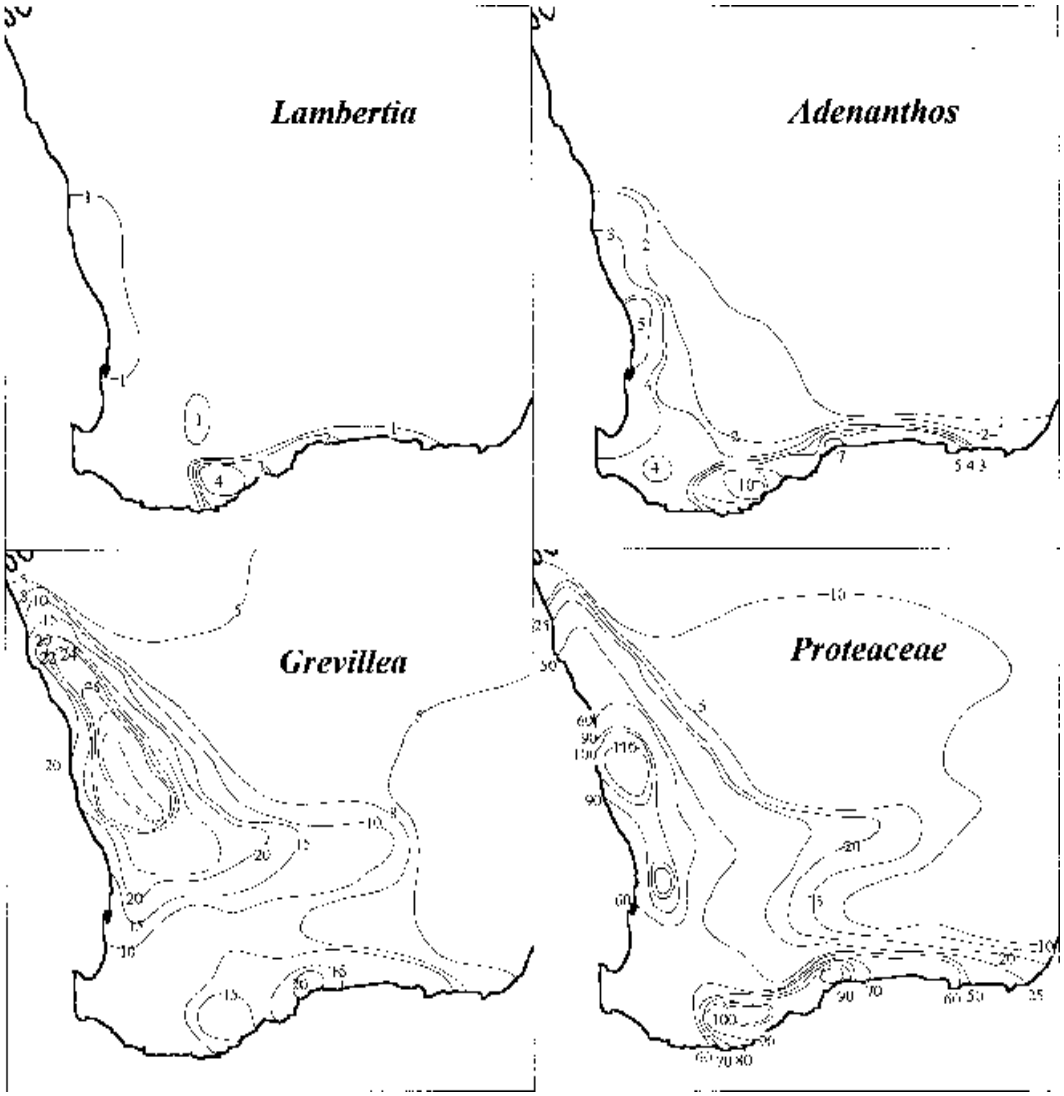

Figure 1. Isoflor maps from Speck (1958) based on a 50000 yard grid; **A**) *Lambertia*, **B**) *Adenanthos*, **C**) *Grevillea* and **D**) Proteaceae.

Some of the small genera such as *Adenanthos* and *Lambertia* exhibited only one main centre of species richness on the south coast while the larger genera such as *Grevillea* exhibited a bimodal pattern of species richness, as did the family as a whole (Fig 1). At both the genus and family level, a feature of the pattern that Speck (1958) showed was the very steep nature of the isoflor gradients away from the centres of species richness.

The more recent analysis of 21000 records held in the Western Australian Herbarium (Fig 2) confirms the general pattern described by Speck (1958). The main difference between the two analyses is the estimate of number of taxa at the centres of species richness (180-194 taxa per grid cell in the current analysis compared with 110-132 taxa per grid cell in Speck's analysis) and the more gradual nature of the species richness gradients now seen. These differences are accounted for by a taxonomy that now recognises more than twice the number of entities recognised in 1958, and the huge increase in collections and access across the south-west that have become available over the last 40 years. The state-wide analysis also shows a small but significant concentration in the Kimberley region, an area not covered by Speck's earlier analysis (Fig 2).

Both analyses show evidence of sample bias. In Speck's (1958) analysis there is a large bulge along Great Eastern Highway that runs from Perth to Kalgoorlie, indicating the poor access north and south off this transport corridor in 1958. The bias in the recent analysis is more subtle, but the small peaks in the arid zone reflect either range systems or major conservation reserves. As a result, it is not possible to unequivocally attribute these small peaks to particular landforms.

Speck (1958) concluded that his isoflor maps supported the theory that the two major centres of high species richness are the centres of origin of the Proteaceae in the southwestern flora. His prediction that the genera of the Myrtaceae and Epacridaceae would reveal essentially similar patterns have been borne out (George 1991; Keighery 1996). Speck (1958) further argued that the high degree of endemism and species richness indicate that these centres of origin were of greater age than if they

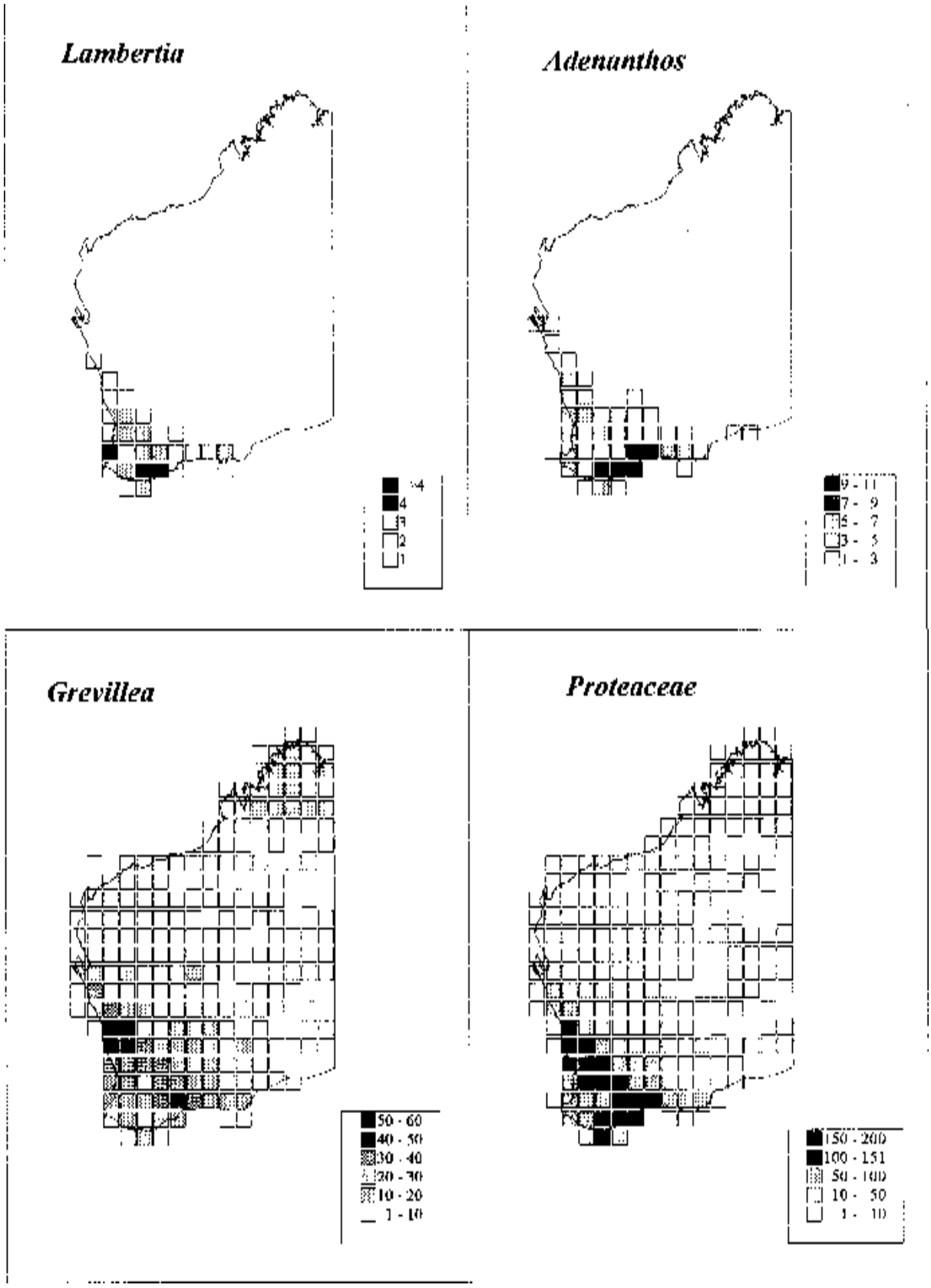

Figure 2. Isoflor maps from a recent analysis of 21000 collections held in the Western Australian Herbarium using one degree grid; **A**) *Lambertia*, **B**) *Adenanthos*, **C**) *Grevillea* and **D**) Proteaceae.

were only refugia and centres of redistribution following an ameliorating climate from the Last Glacial. Hopper's (1979) review of species richness across the southwest suggested that the transitional rainfall zone (in which the two centres of species richness are found) have had an extremely long history of changing climate and the species diversity of this region is a function of the both the stability of the landscape and the repeated pattern of sweeping climatic change, echoing Speck's conclusions of some 20 years previously.

In addition to his analysis of distribution patterns in the Proteaceae, Speck also undertook structural mapping of the vegetation communities across the southwest. He recognised 62 community types in 26 vegetation systems. Using these 26 vegetation systems he proposed modifications to the phytogeographic districts of Diels (1906). These modifications included the eastward movement of the Coolgardie and Austin boundary and the inclusion of a separate Lesueur district. Speck split his southern node of species richness between the Stirling district (which includes the Stirling Range) and the Eyre district (which includes the Fitzgerald River area). Beard's (1980, 1990) later mapping did not recognise the Lesueur district and incorporated all of the southern node of species richness (stretching from the Stirling Range to Fitzgerald River) into his Eyre district.

In a recent analysis of the pattern of biogeography of the genus *Banksia*, Lamont & Connell (1996) argue for the recognition of the Lesueur district, a south Stirling district and a west Eyre district corresponding to centres of *Banksia* species richness and similarity. Our current analysis was undertaken at a coarser scale than that of Lamont & Connell (1996), and only considered species richness; nevertheless, the northern node of species richness seen in our data (Fig 2) is centred on their Lesueur node (Fig 6b in Lamont & Connell 1996). At the one degree grid scale used in our analysis, no subdivision of the southern node of species richness is evident (Fig 2). While phytogeographic boundaries are not based on species richness criteria our data lends some support to a reappraisal of the status of the Lesueur phytogeographic district.

A synopsis of Nathaniel Speck's botanical career

Nathaniel Henry Speck was born in South Australia on 6 December 1906 and died in Canberra in 1970. Speck was one of those rare people who built two successful careers during his life time. The first as a science teacher then secondly as a botanist and ecologist. He began his second career with a BA degree majoring in botany which he started in 1942 at the age of 35. He graduated from the University of Western Australia in 1948. Between 1949 and 1952 he worked on his masters dissertation in which he described and mapped the major plant communities of the Swan Coastal Plain around Perth. At this time he was also responsible for the establishment of the Herbarium at the Botany Department of the University of Western Australia, which played a major role in the development of the illustrated key to the Western Australian flora produced by Blackall and Grieve (Grieve 1953). Speck was awarded his MSc in 1952. He immediately enrolled as a PhD candidate and in 1953 was awarded a Senior Research Fellowship. His PhD topic was very ambitious; he attempted to describe and map the vegetation communities of south-western Australia from Shark Bay to Esperance, and as an aside he undertook a biogeographical analysis of the family Proteaceae across this region.

During this time he continued to assist Professor Grieve with preparation of the illustrated key to Western Australian flora, in redrawing and redrafting some of Blackall's earlier illustrations, and by taking many colour photographs for illustration of those volumes (Grieve 1953).

In July 1953, Speck applied for a position as a Technical Officer with CSIRO's Land Research and Regional Survey Section. It appears that CSIRO was so impressed with his application that they readvertised the position at a Research Officer level and Speck was offered this position, which he subsequently accepted in November 1953 at the age of 47. He and his family moved to Canberra where he commenced work as a Research Officer Grade 3 - Ecologist on 5 April 1954.

Speck immediately fitted into the survey section and undertook field work in the Gilbert-Leichardt area, around Wiluna, Western Australia and in the west Kimberley. He was made permanent in November 1954, and reclassified to Senior Research Officer in 1957. Reports of his ability and performance in CSIRO over this period are uniformly glowing.

Speck was awarded his PhD in 1959 from the University of Western Australia. His thesis was in two parts. Volume 1 described and mapped 62 plant associations in 26 vegetation systems across the southwest of Western Australia. The second volume mapped the distribution of 426 species of Proteaceae across the same area on a 50000 yard grid, and for the first time quantified the patterns of diversity of this family. It is unfortunate that Speck never formally published any of this work and this probably cost him the national and international recognition that he certainly deserved. Speck was by that time 53 years old. His work commitments in a senior position in CSIRO protracted the completion of his thesis which he initially expected to complete it in two or three years before his appointment to CSIRO. It in fact took him over six years to complete.

In the last few years of his professional life, Speck undertook consulting work as a survey ecologist for the United Nations Food and Agriculture Organisation and the UN Development Program in Argentina while on unpaid leave from CSIRO. He retired from CSIRO at the age of 60 on 2 February 1966.

In his second career Speck made a major contribution to the fields of botany, ecology and biogeography in Australia. He made over 8500 collections of which over 1800 are lodged in the Wesrern Australian Herbarium. His published ecological work covered areas as diverse as the Swan Coastal Plain to the north Kimberley to Queensland (Appendix 1). He collected four type specimens (*Eremophila congesta* ms, *Thysanotus speckii*, *Conostylis crassinervia, Grevillea makinsonii)* of which the *Thysanotus* bears his name. He had a life long interest in botany and ecology, collecting and drawing plants wherever he lived. His type collection of *Grevillea makinsonii* was made

the year before he died. With his passing in 1970 at the age of 63, Australia lost one our most significant but unrecognised field ecologists and plant biogeographers.

In his second career, Speck made a very significant contribution to the knowledge of plant biogeography in Western Australia, so much so that many of his insights are now considered common knowledge. Perhaps there is no greater accolade.

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Appendix 1.

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