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Biogeography of *Oxalis* (Oxalidaceae) in South Africa: a preliminary study

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ABSTRACT

Oxalis L., commonly called sorrel, is a large and cosmopolitan taxon that has undergone spectacular speciation within southern Africa (± 270 taxa), and more specifically within the winter rainfall regions of the western Cape Region (CR). The main objective of this study was to analyse the geographical distribution of *Oxalis* in South Africa in relation to currently defined phytogeographic units. The observed patterns of biodiversity and endemism within South African members of the genus show interesting disjunctions and concentrations of species. *Oxalis* is one of the few CR taxa that is shared between the core Fynbos and Succulent Karoo Biomes, and this study therefore provides a novel insight into evolutionary trends across, and not only within, these phytogeographic units. The major centre for diversity for *Oxalis* is situated on Table Mountain and the northern areas of the Cape Peninsula (grid square 3318CD). Subsidiary centres are located in the Clanwilliam/Niewoudtville and Kamiesberg regions. The reported patterns in Western Cape suggest that *Oxalis* species richness has been generated and retained in areas which have been identified as core Fynbos (Table Mountain), Fynbos refugia during interglacials (Kamiesberg), and an ecotonal region which might switch between the two biome types (Clanwilliam/ Niewoudtville). Presumably these three types of areas would provide interesting material for DNA-based phylogenetic work, and a test of the climate change 'species-pump' hypothesis proposed by Midgley *et al.* (2001).

INTRODUCTION

Oxalis L. (Oxalidaceae) is a large and cosmopolitan genus, including more than 800 species (Chant 1993). Most of its range is covered by a limited number of species, such as *O. pes-caprae* L. and *O. corniculata* L., which are ubiquitous weeds (Salter 1944).

Oxalis has two well-developed centres of diversity, which represent over 90% of the species. One centre is located in South-Central America, including more than 500 species. The other is in South Africa, more specifically within the Cape Region (CR) (Cowling & Hilton-Taylor 1997), where ± 150 species are found in an area of less than 90 000 km^2, with extensions both northwards and eastwards along the coast. In total, southern Africa hosts ± 270 *Oxalis* taxa (Dreyer 1996). The Cape Region, as defined by Cowling & Hilton-Taylor (1997), coincides with the Fynbos Biome, but also includes enclaves of karoo and forest, which form part of the Succulent Karoo and Forest Biomes respectively (Rutherford & Westfall 1986).

There has been a tremendous degree of speciation among the CR representatives. A number of other families and genera with cosmopolitan distributions exhibit similar patterns of massive speciation within the region. Examples include the Proteaceae, with 330 species in the region, as opposed to roughly 70 species within the rest of Africa (Rebelo 1995), the Restionaceae with 275 species (Cowling & Richardson 1995), the Mesembryanthemaceae, with 1 800 species (Smith *et al.* 1998) and the genus *Erica* L., with 658 species (Goldblatt & Manning 2000).

Possible reasons for the dramatic speciation within the CR have been suggested (Linder 1985; Cowling *et al.* 1992). A combination of topographic gradients (Linder *et al.* 1992) and the regular occurrence of fire (Cowling 1987) have been suggested as the main driving factors towards speciation, although the latter two explanations are not entirely appropriate for the Succulent Karoo Biome, which forms part of the CR. More recently, evidence has been published supporting the 'species pump' hypothesis (Midgley *et al.* 2001) that Pleistocene climate change played a role in determining plant species richness and phytogeographic patterns in the greater Cape Mediterranean region (Goldblatt 1978). Although some work has been done on the distribution of plant species within the CR, it has focused almost exclusively on taxa predominantly confined to the Fynbos Biome, the typical but not exclusive vegetation type of the CR (Oliver *et al.* 1983). Despite some cursory observations by Salter (1944), very little has been published on the distribution of *Oxalis* within South Africa. The aim of this study was to map the distribution of this genus within South Africa, and to analyse the geographical distribution of *Oxalis* in South Africa in relation to currently defined phytogeographic units.

MATERIALS AND METHODS

Data on the distribution of *Oxalis* were obtained from Salter (1944) and the Pretoria Computerised Information System (PRECIS) database. These data were provided in 16th degree grid square increments, and provided distributional information for 237 of the 270 taxa. This is currently the most complete and up-to-date list of biogeographical data available for the genus, given the taxonomic uncertainty within several sections of *Oxalis*. Nevertheless, the total of 237 represents ± 88% of even the most comprehensive list of *Oxalis* taxa, and is thus considered adequate to represent the entire genus within

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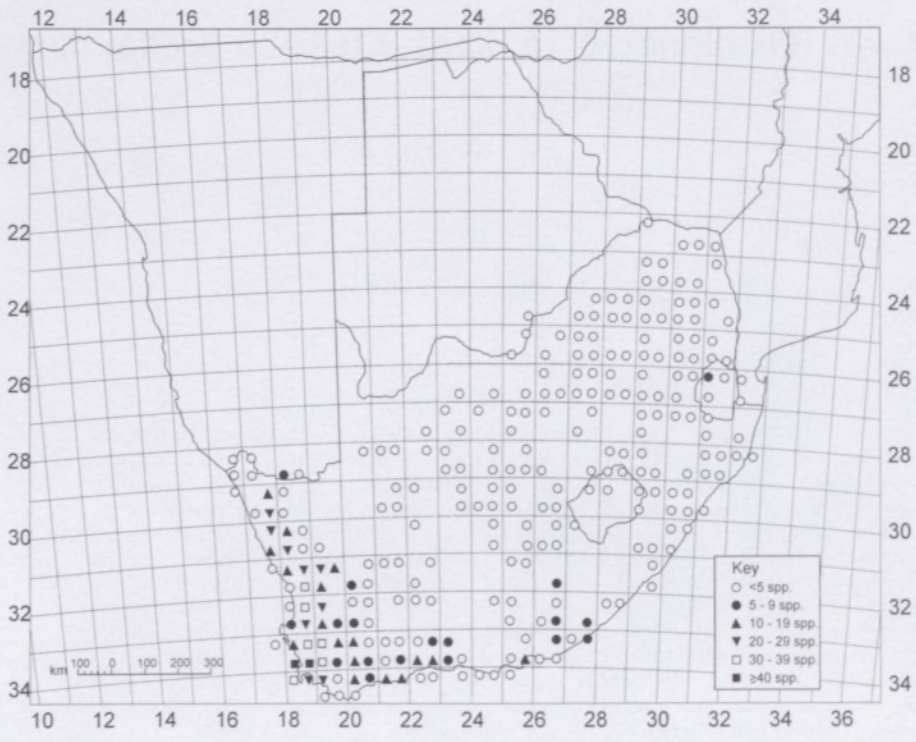

FIGURE 1.—*Oxalis* diversity in South Africa.

the country. Most of the taxa not included are taxonomically unresolved or vague.

Totals for each 16th degree grid square (which would provide taxon numbers for that grid square i.e. richness) and for each taxon restricted to only one, or two adjacent, 16th degree grid squares (i.e. reasonable marker for endemism levels) were extracted.

These data were then summarized at quarter degree grid square level, and the repeats eliminated. The figures were transferred to the appropriate grid squares on maps of South Africa.

RESULTS

Oxalis is distributed throughout the study area (Figure 1), with an observed increase in diversity and endemism levels to the south and west of South Africa (with the notable exception of the Great Karoo), culminating within the CR, where the vast majority of taxa are located. This pattern is a classic example of the distribution of many prominent CR families and genera.

Three centres of diversity were identified. The largest and most speciose is positioned on the Cape Peninsula, extending to the Kogelberg/Hottentot's Holland Mountain Ranges to the east. Although the two ranges are separated by the Cape Flats, they are considered as a single unit for the purposes of this project, because of the high degree of *Oxalis* species shared between them (60%).

A secondary centre of diversity is situated in the Clanwilliam/Niewoudtville region. Although not as speciose as the Hottentots Holland epicentre, this region contains a wide range of unique species, both within *Oxalis* and in other taxonomic groups (Schumann & Kirsten 1992; Rebelo 1995). This epicentre is higher in altitude and further inland than the Cape Peninsula, and thus has a somewhat different, more arid, climate.

The third main centre of *Oxalis* biodiversity is situated in the Kamiesberg region of the Northern Cape. This is a region of extreme botanical interest as the unique Namaqualand and Richtersveld areas, containing many semi-desert paleo- and neo-endemics, surround it. In addition, the region still harbours fynbos taxa (Cowling & Pierce 1999), probably isolated there after the retreat of the last glacial maximum (Midgley *et al.* 2001).

Other minor centres of diversity occur throughout South Africa, but at least two can be considered somewhat biased as they are located near or on major cities, and have therefore been extensively collected. These two sites are located on the Witwatersrand and on Algoa Bay grid squares, the first containing the cities of Johannesburg and Pretoria and the latter the city of Port Elizabeth. The Cape Peninsula centre probably also shows some collecting bias, as it is located on a major city, and is the site of South Africa's main Botanical Gardens at Kirstenbosch. Collection records for the Cape Peninsula are probably much better than for Namaqualand, in part due to the brief and ephemeral appearance of *Oxalis* species. Collectors in more remote areas, which are visited only occasionally and not on such a regular basis as areas around Cape Town, may easily miss these plants. At present no reason can be offered for the existence of other sites, such as the one located in Swaziland and in the East London/Umtata area. The last centre, located on the eastern Langeberg/Outeniqua, could possibly also be a southern Cape refugium.

Oxalis is represented throughout most of the rest of South Africa by only six species, namely *O. depressa* Eckl. & Zeyh., *O. obliquifolia* Steud. ex Rich., *O. obtusa* Jacq., *O. semiloba* Sond., *O. smithiana* Eckl. & Zeyh., and the naturalized American species *O. corniculata* L.

All taxa confined to one, or to two adjacent 16th

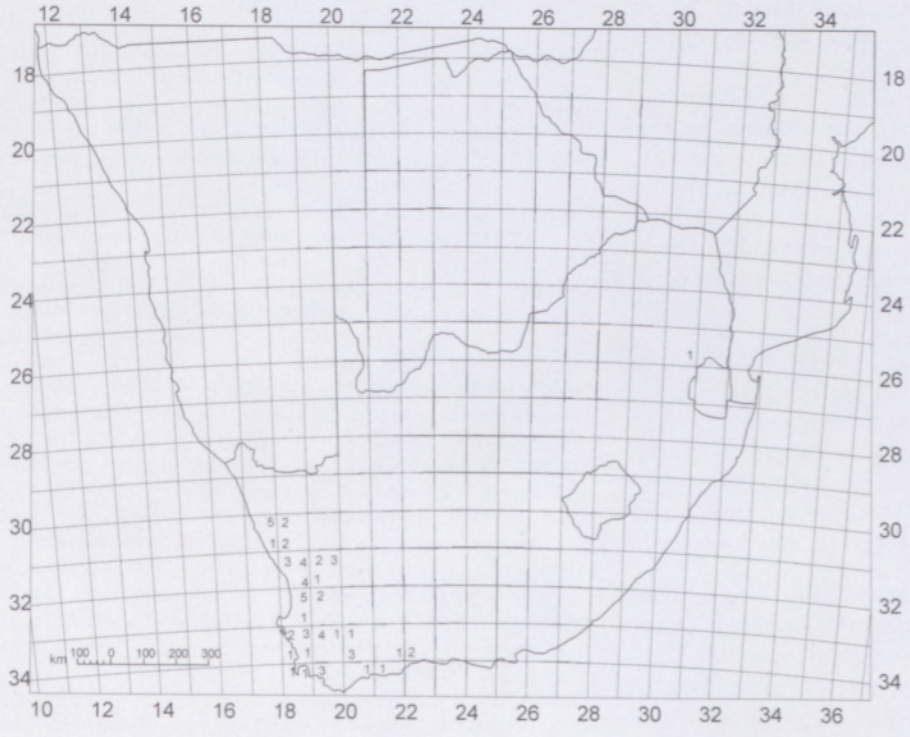

FIGURE 2.—*Oxalis* endemism in South Africa. The numbers refer to the number of endemic species within each quarter degree square.

degree grid squares were considered adequate to represent local scale endemism (Figure 2). Several of the diversity centres are confirmed as centres of endemism, such as the Hottentots Holland, Clanwilliam/Niewoudtville and southern Cape centres. The most speciose square, centred on Table Mountain, contains only one endemic species, which is a surprisingly low value. However, this might be an artefact of scale. The Kamiesberg Centre is not represented. A species regarded as endemic according to our criteria, occurs within southern Mpumalanga, in grid square 2530D. *Oxalis davyana* Knuth is a taxonomically isolated species assigned to a monotypic subsection (Section *Eu-cernuae* subsection *Goetzea*) by Salter (1944), and is biogeographically equally isolated from other centres of endemism.

The top ten hot spots, defined as the ten most speciose squares at 16th degree grid square level, all feature more than 20 species, with four containing 30 species or more (Table 1). Between them, these ten squares contain 137 taxa, ± 58% of the total complement. The most speciose square, centred on Table Mountain, contains 40 species, over one sixth of the total in the database. These areas are top priorities for conservation, at least in terms of *Oxalis* (Rebelo 1994). As mentioned previously, it should be noted that several, if not most of these areas are heavily subject to collecting bias, but this does not invalidate their essential conservation value.

TABLE 1.—Ten most speciose grid squares: *Oxalis* diversity from the PRECIS database

Grid square	Region	No. spp.
3318 CD	Table Mountain	40
3318 DD	Stellenbosch	32
3418 AB	Southern Cape Peninsula	31
3218 BB	Clanwilliam	30
3318 DB	Paarl	28
3017 BB	Southern Kamiesberg	25
3318 DC	Bellville	21
3319 AC	Tulbagh	21
3119 AC	Niewoudtville	21
2917 DB	Northern Kamiesberg	21

DISCUSSION

Oliver *et al.* (1983) have provided a recent comprehensive analysis of CR phytogeography, including a distributional analysis of 1 936 species in Fynbos Biome families. According to this analysis, a typical CR taxon would show a maximum centre of diversity within the Caledon District; more specifically the Kogelberg massif located in grid square 3418BB, with species numbers and endemism levels tailing off towards the north and east. Despite the huge sample size and the undoubted value of the Oliver *et al.* (1983) analysis, their approach has been criticized for focusing exclusively on Fynbos families and ignoring the other major biomes of the CR, namely Succulent Karoo and Afromontane Forest (Bayer 1984). As has been noted by various authors (Levyns 1963; Cowling & Hilton-Taylor 1997), the floras of the three biomes (Rutherford & Westfall 1986) are taxonomically distinct at virtually every level and very few genera are shared between them. *Oxalis* provides a useful exception, in that it is one of the few taxa that is shared between the core Fynbos and Succulent Karoo Biomes. Some others include members of the genus *Pelargonium* L'Hér., section *Hoarea* DC. (Marais 1994), *Crassula* L. as well as certain members of the Mesembryanthemaceae, such as *Ruschia* Schwantes and *Lampranthus* N.E.Br. (Jurgens 1991). It is notable that all of these taxa are adapted to a geophytic or succulent lifestyle.

Midgley *et al.* (2001) point out that geophytic growth forms are resilient to the drought and fire disturbance regimes that characterize both biomes. This would have enabled geophytes to thrive even during periods of climatic change and associated successive replacements of the Succulent Karoo and Fynbos Biomes with one anoth-

er during Pleistocene fluctuations. They offer this as an explanation for the hitherto unexplained diversity of geophytes at the interface between the two biomes. *Oxalis*, which is geophytic in southern Africa, fits this pattern. Thus the most unusual feature of *Oxalis* distribution, the strong representation along the west coast and subsidiary centres of diversity within the Clanwilliam/Niewoudtville and Kamiesberg areas, is easily explained. Bioclimatic modelling suggests that they were some of several fynbos refugia maintained over the last glacial period (Midgley *et al.* 2001).

It is notable that the centre of diversity for *Oxalis* is not situated in the grid square 3418BB, highlighted by Oliver *et al.* (1983), as is the case for many other Fynbos families. The most diverse centre is, in fact, further north and west, on the drier plains of the Boland and West Coast (Table 1). Grid square 3418BB is notably absent from the list of ten most speciose grid squares for *Oxalis*.

Several authors, including Levyns (1963), have indicated that the centre of diversity for the Succulent Karoo is further north and west, to the drier, more Mediterranean parts of the CR, than the typical Fynbos centre. Although *Oxalis* is not a pure Succulent Karoo taxon, our data are consistent with such a conclusion.

In this paper, several of the diversity centres are also confirmed as centres of endemism, such as the Hottentots-Holland, Clanwilliam/Niewoudtville and southern Cape. The fact that the Kamiesberg Centre does not contain *Oxalis* endemics could be due to the recent nature of its isolation from the southwestern Cape region in terms of climate and flora. The Kamiesberg Fynbos outlier may have been isolated for only roughly 12 000 to 15 000 years (since the end of the Pleistocene). This could mean that not enough time has elapsed for consequent genetic isolation and speciation to occur. This is supported by observations in other families in the region. Of the seven *Erica* species that occur on the Kamiesberg, all seven are also represented further south (Cowling & Pierce 1999), and both Proteaceae species, although endemic, are closely related to southern species (Rebelo 1995; Reeves 2001).

In conclusion, *Oxalis* is one of few genera that exploit both the Succulent Karoo and Fynbos Biomes successfully and prolifically. Thus this genus provides an excellent opportunity to assess various hypotheses relating to diversification in the CR. Richardson *et al.* (2001) produced the first DNA phylogeny that suggests a recent rapid floristic diversification in the CR. The geographic distribution of taxon richness within *Oxalis* discussed in this paper, sets the stage for further promising DNA-based phylogenetic work in this region. Such an approach will be critical in developing an understanding of the factors responsible and the time scales involved in the genesis of the floristic biodiversity hotspots of the fire-prone Fynbos and drought-prone Succulent Karoo Biomes.

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