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From Alpha Taxonomy to Genomics in South Africa: One of the hottest biodiversity hotspots

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Abstract

South Africa is home to globally important plant diversity, with over 20,000 species of vascular plants among which 57% are endemic, including three biodiversity hotspots. The south western part of the country holds over 50% of the species in the Cape Floristic Region and Succulent Karoo hotspots, comprising Mediterranean vegetation that has been mostly assembled since the Miocene. To the east, the Maputaland-Podoland-Albany hostpot region has summer rainfall and vegetation similar to tropical Africa. Botanical exploration started in the 1700s, with collectors including Carl Thunberg, and species discoveries continue to date. Nearly 3 million herbarium specimens are housed at the South African National Biodiversity Institute (SANBI), at universities, at museums, and in nature reserves. The majority of the specimens within the SANBI and selected large herbaria elsewhere have been databased and images of types and other collections are available online. Relative to other parts of Africa the molecular systematics revolution has been actively adopted with several of the hotspots reasonably studied, more recently as part of the DNA barcoding initiative. Comparative studies, linking the herbarium collections and using DNA (sources include botanic gardens), address questions on the origin and assembly of the unique biodiversity. A recent strategy for plant taxonomic research outlines goals towards achieving targets of the Global Strategy for Plant Conservation, including production of an e-Flora and highlighting priority plant groups for taxonomic study. There are some dedicated funding streams towards achieving these goals, but the plant taxonomy enterprise is frustrated by low numbers of active taxonomists (1 person per 500 species), reduced training in systematics and low uptake of newer approaches.

Key Words: herbaria, new species, plant collectors, research strategy, southern Africa, systematics

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Africa's vegetation is diverse and has been grouped into various biomes and up to 18 phytochoria (White 1983). The continent's biota were grouped into four major biogeographical clusters: the Guinea-Congolian, Southern African, Zambezian to Horn of Africa, and the Saharan to Nubian Desert (Linder *et al.* 2012). Within southern Africa four smaller units (i.e., Cape, Natal, Kalahari and Namib elements) were recognized, all represented in South Africa.

South Africa is one of the most biodiversity rich countries in the world. With a size of about 1,214,000 km^2 (http://www.worldatlas.com), about twice the size France, the country hosts nearly 20,000 species of vascular plants (Klopper *et al.* 2007). This diversity is structured into five major biomes (Fynbos, Succulent Karoo, Albany Thicket, Grasslands, Savanna; Mucina & Rutherford 2006). There is uneven distribution of vascular plants among these biomes, with the Fynbos biome being most rich and holding about 9000 species in an area of about 90,000 km^2 (Manning & Goldblatt 2012). Also the vascular flora has high endemicity, with about 13,300 species restricted to South Africa nearly half of which are restricted to the Fynbos biome.

The high diversity of species in South Africa is linked to its geology, climate and interactions between abiotic and biotic factors. Geologically, the country sits on an old landscape which has been relatively stable except for Palaeozoic processes such as folding leading to the Cape mountains as well as more recent (Miocene) uplifts leading to formation of the Drakensberg mountains (Linder & Verboom 2015). Varying erosion and shifts in drainage system, together with shifts in sea levels, have led to a complex geology especially in the Cape area (Cowling *et al.* 2009). Within the Miocene, upwelling of the Benguela current (Dupont *et al.* 2011, 2013; Hoetzel *et al.* 2013) triggered a shift in rainfall seasonality, with winter rainfall becoming prevalent in the south-western areas whereas the eastern and northern parts of the country experienced summer rainfall. Consequently, the vegetation has shifted from a tropical woodland in early Miocene (Linder & Verboom 2015) to the currently observed biomes which are partitioned into the winter rainfall areas (Fynbos, Succulent Karoo; collectively referred to as the Greater Cape Floristic Regions (GCFR)), and summer rainfall area with no winter snow (savanna), and summer rainfall with winter frost (Grasslands, Nama Karoo).

Botanical Collections in South Africa

Southern Africa has a rich history of botanical explorations (Glen & Germishuizen 2009). The region attracted botanical collectors since the 16th century, with the first known vascular plant record being an illustration published in Leiden in 1605 of a dried inflorescence of *Protea neriifolia* R. Br. in the *Exoticorum libri decem* (Clusius 1605). The importance of the Cape, as a restocking point for voyages enroute to Asia, encouraged earlier collections and plants from this region gained popularity among pre-Linnaean collectors and gardeners. The publication of the *Species plantarum* (Linnaeus 1753), beginning the binomial naming and seeking to catalogue all know biodiversity, injected impetus to the naming and classification of biodiversity. Carl Thunberg, a student of Linnaeus, arrived in the Cape in 1772 and made three journeys travelling into the interior where he collected about 3100 specimens (kept as part the historical Thunberg Herbarium at the University of Uppsala, UPS-THUNB), and this comprises one of the earliest focussed collections from southern Africa. During the 19th century, specimens were collected and distributed to a number of European institutions, notably by collectors such as C.F. Drège, C.F. Ecklon and C.L.P. Zeyher. With the establishment of colonies (Cape, Natal), collectors based within the region accumulated specimens leading to establishment of precursors of current day herbaria (codes follow Thiers continuously updated) at Cape Town (South African Museum Herbarium, SAM), founded 1825; Bolus Herbarium (BOL, founded 1865), Grahamstown (Selmar Schonland Herbarium, Albany Museum (GRA, founded 1855), and Natal (KwaZulu-Natal Herbarium, Durban (NH, founded 1882). Notable 20th century collectors include E.E. (Elsie) Esterhuysen, who collected over 34,000 specimens with a bias on Cape flora and who is celebrated in over 60 species names. Robert H. Compton collected 35,000 specimens, perhaps the highest number of specimens in Southern Africa, among which 8000 were from Swaziland, and his collection forms part of the Compton Herbarium (NBG, which now also includes the South African Museum Herbarium, SAM). The history of botanical collections were strongly influenced by political history at local to international levels, and are intertwined with personalities wielding power and influence over the last three centuries (Carruthers 2011). It is interesting

Table 1: The largest herbaria in South Africa. * Mycological collection.

Province	Institution	Established	No. of specimens
Gauteng	National Botanical Institute (PRE)	1903	1,200,000
Western Cape	National Botanical Institute (NBG)	1933	500,000
Western Cape	University of Cape Town (BOL)	1865	300,000
Eastern Cape	Albany Museum (GRA)	1855	200,000
KwaZulu Natal	University of KwaZulu-Natal (NU)	1910	120,000
KwaZulu Natal	National Botanical Institute (NH)	1882	100,000
Gauteng	University of the Witwatersrand (J)	1917	100,000
Gauteng	University of Pretoria (PRU)	1924	100,000
Gauteng	Agricultural Research Council (PREM)*	1905	60,000
Northern Cape	McGregor Museum (KMG)	1908	32,600
North West	University of North-West (PUC)	1932	28,000
Free State	National Museum Herbarium (NMB)	1984	25,000
KwaZulu Natal	KwaZulu-Natal Nature Conservation Service (CPF)	1985	23,100
Free State	University of the Orange Free State (BLFU)	1905	20,000
Northern Cape	Grootfontein Agricultural College	1911	20,000

to note among the collectors were the two-times Prime Minister of South Africa (Jan C. Smuts), but it is disconcerting that only 1% of the 2000 plant collectors are black Africans.

There are over 70 herbaria in South Africa which together hold about 3.1 million specimens (Smith & Willis 1999; Table 1). The South African National Biodiversity Institute (SANBI) manages several of the largest herbaria (National Herbarium, Pretoria, PRE; Compton Herbarium, Claremont, NBG; KwaZulu-Natal Herbarium, Durban, NH) which hold nearly 60% of the specimens. About 90% of the collections are housed at the top ten largest herbaria which are part of SANBI or at universities, and nearly 50% of the herbaria have less than 10,000 specimens. These collections have varying usages, with the majority of the small collections held at nature reserves and focused on biodiversity within a small region or dedicated to particular kinds of plants, e.g., weeds or agricultural species. In addition to herbarium collections, there are a number of botanic gardens especially under the SANBI network, distributed in all the provinces.

Recent Trends in Capturing Specimen Data and Images

Information on herbarium specimens is unavailable to wider usage if it only exists as physical specimens in the holdings of a particular institution. Within the last two decades, various efforts have been made to provide such data in alternative forms, ranging from databases to completely searchable images. Specimens held under the SANBI herbaria are databased and information can be searched online with options to compile maps and sieve other details linked to the data. The South African Biodiversity Information Facility (SABIF) is a participant in the global collation of data on various taxa, and there has been concerted effort to capture data from herbaria and other repositories outside the SANBI network. More recently, South Africa herbaria participated in the African Plant Initiative (API) project, contributing immensely to the wealth of type specimens. Outside the SANBI network, the Bolus Herbarium (BOL) at the University of Cape Town, founded 1865, has a large collection of 11,500 types of the Cape Flora, holding one of the oldest and perhaps richest historical collections in the country.

The contribution of citizen scientists in biodiversity information gathering has been recognized widely. There is extensive involvement of the wider public in gathering images and other data on various biota, particularly animals, and such data forms a unique resource in gazetting the occurrence of various taxa. The South African virtual museum (http://vmus.adu.org.za/) has a wide variety of animals, but is rather poor on plants. Better plant content is at iSpot (www.ispotnature.org/communities/southern-africa), a forum used by amateur botanists to deposit images and data. The potential of involving citizen scientists is as yet to be fully exploited.

Species Discovery, Catalogue of Taxa into Floras

The discovery, description and cataloguing of new taxa to science continues into the 21st century. The earliest catalogues of the southern African flora goes back to Thunberg's *Prodromus plantatrum Capensium* (Thunberg 1794-1800), which was followed by the several volumes of *Flora Capensis* (Harvey, Sonder *et al.* 1860-1933). Unlike tropical Africa where regional floras (e.g. *Flora of Tropical East Africa*) have attempted to provide detailed description of each species, there is no single detailed regional flora for South Africa. Instead there are lists of species in national checklists (e.g., Germishuizen *et al.* 2006), and at a regional scale (e.g. biome or province), the most recent being the two volume conspectus of the Greater Cape Flora (Manning & Goldblatt 2012; Snijman 2013). Various publications on the flora are being collated under the e-Flora of South Africa, which contributes to the mandate on the Global Strategy for Plant Conservation, 2011-2020 (GSPC; https://www.cbd.int/gspc).

Despite the long collecting history, new species are still being recorded due to detailed inventory in previously under-collected areas as well as from specimens already incorporated into herbaria. A survey of publications on new species in the *South African Journal of Botany* (SAJB) for the period 2005-2015 reveals that over 121 species endemic to South Africa were described (Fig. 1). These mostly belong to the Asteraceae (20 species) and Fabaceae (20), Iridaceae (16), Apiaceae (12), and are predominantly from the GCFR (69%) and a third were geophytes. Recent sustained fieldwork in previously under-collected areas, such as the quartz fields of the Namaqualand and Overberg (e.g., Curtis *et al.* 2013), has contributed most to the increased discoveries.

Adoption of Molecular Data

Molecular phylogenetic approaches, mostly based on Sanger sequencing, have been adopted in the study of the South African flora. These include studies inferring phylogenetic relationships among lineages, origin and biogeographic patterns, and relating to the monophyly and classification of suprageneric taxa. There is evidence of complex radiations leading to the flora in the fynbos, desert, grasslands and woodlands since the Miocene (Linder & Verboom 2015), most notably the shift from tropical/subtropical woodlands to the current temperate flora in the hyper diverse winter rainfall area. There is consensus that observed biogeographic links between the austral-temperate continents has occurred by long distance dispersal since the split of Gondwana (Crisp *et al.* 2009), and there are frequent exchanges of species between similar habitats (Linder & Verboom 2015).

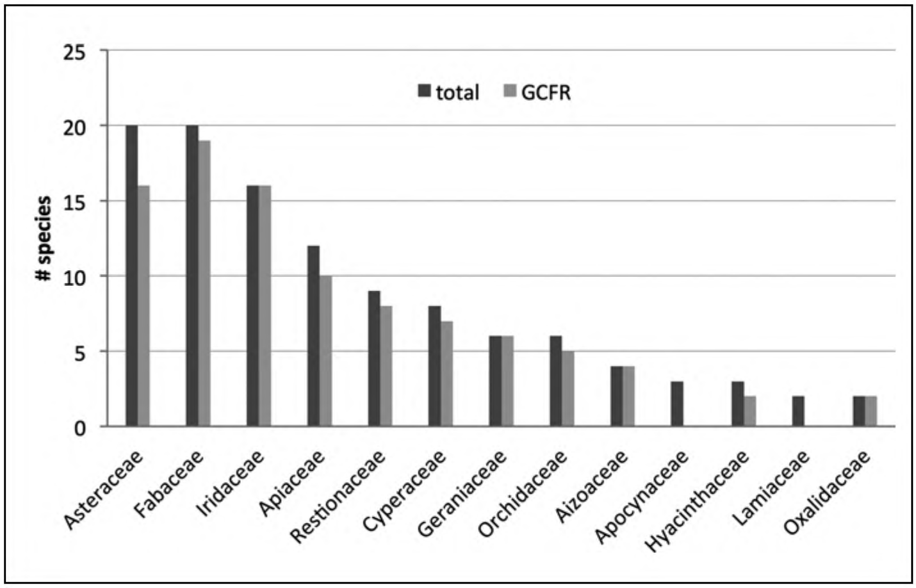

Fig. 1. A summary of new species published in the *South African Journal of Botany* during 2005–2015. GCFR: Greater Cape Floristic Regions.

Adoption of DNA sequencing approaches in taxonomic studies has focused mostly at suprageneric level. There are ongoing revisions of generic circumscriptions, especially among widespread genera, which have been found not to be monophyletic. As a consequence, a number of genera have been enlarged to include previously segregated lineages (e.g., *Cyperus*: Bauters *et al.* 2014; Larridon *et al.* 2011). In several cases, large genera have been split into smaller units in attempts to achieve monophyly by recognizing smaller (and at times charismatic subgroups) especially in economically and horticulturally important taxa such as *Aloe* (Manning *et al.* 2014). Within the last 10 years, four small genera (*Bertilia*: Cron 2013; *Dracoscirpoides*: Muasya *et al.* 2012; *Kappia*: Venter *et al.* 2006; *Wiborgiella*: Boatwright *et al.* 2010) have been described in the SAJB to segregate previously known taxa that had been included in larger (non-monophyletic) taxa, in all four cases based on re-interpretation of morphology in combination with DNA sequence data. More generic changes can be expected as more taxa are included in broader studies especially in transoceanic disjunct genera occurring in austral-temperate areas.

DNA barcording is gaining popularity in the study of the southern African flora. Spearheaded by the African Centre of DNA Barcoding, over 15,000 DNA barcodes (van der Bank *pers. com.*) have been deposited at the global database (Consortium for the Barcoding of Life, CBOL) for the two main plant barcodes (*rbcL*, *matK*). The South African barcodes have targeted groups such as woody and invasive species as well as major plant families such as the legumes and sedges. These DNA barcode data have been used to address questions relating to community assembly processes (e.g., Maurin *et al.* 2014), phylogenetic diversification (e.g., Bello *et al.* 2015), and invasion biology (e.g., Bezeng *et al.* 2015). Despite the perceived utility of DNA barcode data (Kress *et al.* 2015), there is lack of divergence among lineages which have experienced recent and rapid radiation such as Cape legumes (*Aspalathus* L., Edwards *et al.* 2008; Psoraleeae, Bello *et al.* 2015).

The adoption of modern approaches in plant taxonomy is restricted to a handful of institutions, where final steps of the Sanger sequencing are outsourced outside Africa. Next generation sequencing and sequencing of whole genomes is yet to become routine in studies of South African plants. Given the high costs of such approaches and the need for bioinformatics skills to analyse the data, it is unlikely that whole genome and next generation sequencing will be adopted widely in the near future. Furthermore, large proportions of budgetary allocation from government are dedicated to poverty alleviation and policies on the green economy are yet to be fully implemented.

National Priorities on Biodiversity Studies

The South African National Biodiversity Institute's mandate includes coordinating and promoting taxonomy on indigenous biodiversity as well as managing herbaria (www.sanbi.org). As part of this mandate, SANBI has undertaken a review of the status of taxonomic research in the country, concluding that: (i) there are under 50 active taxonomists (a third of them already retired) and several unfilled posts due to government policies on equity; (ii) there is a decline in number of large revisions but there is steady description of new taxa as stand-alone or in papers revising small groups of species; (iii) the ratio of number of species to taxonomists is about 500 species to one; and (iv) nearly 3800 species are represented by under five specimens in herbaria (Victor *et al.* 2015a). The human resource shortage is exacerbated by low uptake of undergraduate studies in taxonomy, and the unequal distribution of taxonomists (and curricula), with few traditionally black universities offering postgraduate training in taxonomy (Victor *et al.* 2015b).

Regardless of the above, South Africa is committed to meet the targets set by the Global Strategy for Plant Conservation (GSPC; www.cbd.int/gspc/). Objective 1 of the GSPC requires that plant diversity is well understood, documented and recognized by 2020. A recent strategy for plant taxonomic research in South Africa (2015–2020; Victor *et al.* 2015a) identifies strategic objectives and proposes three research programmes. Research programme 1 aims to produce an online (e-Flora) for South Africa, focusing on 13 large families (Aizoaceae, Asphodelaceae, Asteraceae, Campanulaceae, Ericaceae, Fabaceae, Geraniaceae, Lobeliaceae, Oxalidaceae, Santalaceae, Scrophulariaceae and Thymelaeaceae), where capacity for research and curation exists at SANBI and local universities. Additionally, priority was identified for understudied families (Cyperaceae, Hyacinthaceae, Malvaceae, Rhamnaceae, and Rutaceae), in which over 50 taxa have not been revised in the last 50 years. Research programmes 2 and 3 set priorities for further studies to revise plant genera that have not been studied since the World War II; genera that have a high proportion of unidentified specimens or have data deficient taxa; genera with economic important species; and genera with a high proportion of taxa occurring in South Africa. These programmes act as a guide in setting priority for gaps in knowledge, and allow funding opportunities from the National Research Foundation to be harmonized with research needs, as evident from recent 'ring-fenced' opportunities under the Foundational Biodiversity Information Programme.

Conclusions

Despite the extended history of plant collecting in South Africa, there remains gaps in the knowledge and new species continue to be described. There are rich collections, with over 3.1 million herbarium specimens made over the last 150 years, which have been databased and are widely available. With over 20,000 species of vascular plants and under 50 active taxonomists, innovative approaches are needed to meet the South Africa's targets under the GSPC. The recently published research strategy and dedication of funding to support the activities will contributes towards a better understanding of the flora.

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