The distribution of the dwarf succulent genus
*Conophytum* N.E.Br. (Aizoaceae) in southern Africa

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**Background:** The dwarf succulent genus *Conophytum* N.E.Br. is one of the most species rich in the Aizoaceae. The genus is most closely associated with a region of high floral endemism and biodiversity, the Succulent Karoo biome in south-western Africa.

**Objectives:** To examine the distribution of *Conophytum* in south-western Namibia and in the Northern and Western Cape Provinces of South Africa.

**Method:** A database comprising 2798 locality records representing all known species and subspecies of the genus *Conophytum* has been constructed.

**Results:** The genus is primarily restricted to the arid winter-rainfall region of the Northern and Western Cape Provinces of South Africa and south-western Namibia, within the Greater Cape Floristic Region. Whilst taxa are found across all the main biomes in the region (the Succulent Karoo,Nama Karoo, Desert and Fynbos biomes), 94% of *Conophytum* taxa are found only in the Succulent Karoo biome and predominantly (88% of taxa) within South Africa. Endemism within specific bioregions is a feature of the genus and ~60% of taxa are endemic to the Succulent Karoo. Approximately 28% of all taxa could be considered point endemics. Whilst the genus has a relatively wide geographical range, we identify a pronounced centre of endemism in the southern Richtersveld.

**Conclusion:** The genus *Conophytum* can be used as a good botanical model for studying patterns of diversity and speciation in the Succulent Karoo biome, the effects of climate change on dwarf succulents, and for informing conservation planning efforts.

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**Introduction**

The environmental conditions in south-western Africa have resulted in a unique flora well adapted to those conditions. The resulting flora is dominated by a large number of leaf succulents, notably members of the Aizoaceae and Crassulaceae (Cowling & Hilton-Taylor 1999). The area is strongly species rich with approximately 5000 vascular plant species recorded for the Succulent Karoo biome, an area of 116 000 km$^2$ that is recognised as a global biodiversity hot spot (Driver et al. 2003). Within the Aizoaceae, a high degree of speciation is evident, no more so than in the miniature or dwarf succulent genus *Conophytum*, with 165 recognised taxa of which 108 are recognised at the species level (Hammer & Young in press). The miniaturisation of growth form in leaf succulents (as seen in *Conophytum*) is an adaptation unique to the region and most evident in the Succulent Karoo biome (Desmet & Cowling 1999a).

In the Succulent Karoo, the combination of high temperatures, low humidity and low cloud cover is characteristic, especially inland from the coastal strip where the temperature range is reduced compared to further inland. The biome itself is characterised by a low winter rainfall (Desmet & Cowling 1999b), with rainfall levels declining east to west and south to north. Matimati et al. (2012) concluded that non-rainfall moisture was a vital element in sustaining dwarf succulents. Fog makes a substantial and reliable contribution to total moisture levels, especially on the west coast. The contribution made by dew to moisture availability is less well understood, although it is much more widespread and less localised than the effects of fog (Matimati et al. 2012).

The highest levels of floristic species diversity within the region, especially amongst dwarf succulents, are commonly associated with koppies or rocky outcrops, which are often small in extent or isolated (Desmet & Cowling 1999a). Such biodiversity is coupled with high levels of endemism with approximately 40% of plants restricted to the Succulent Karoo biome. The flora is further characterised by high numbers of local or range-restricted endemics (Cowling & Hilton-Taylor 1994; Hilton-Taylor 1996). At its extreme, point endemism is most pronounced amongst succulents, especially members of the Aizoaceae, notably in *Conophytum* (e.g. Desmet, Ellis & Cowling 1998;
Ihlenfeldt 1994). Plant form varies widely within the dwarf succulent guild, and several morphologically defined Sections are recognised in *Conophytum* as a result (Hammer 1993, 2002; Hammer & Young in press).

The genus *Conophytum* occupies a wide range of habitats, from the quartz-pebble-rich plains of the Knersvlakte through the high, granite-dominated mountains of the Khamiesberg to the quartz inselbergs of Bushmanland and the southern Namib Desert. The plants are rarely found in large or dense communities but are rather widely dispersed amongst other succulent shrubs or occupy discrete habitat niches, for example, small rocky outcrops in large sandy plains, the edges of shallow grit pans, shaded (south-facing) lichen-covered granite slopes or flat gravel plains (Figure 1). The area occupied by many *Conophytum* populations is therefore often small, to the extent that such small populations may not always be recognised by current national vegetation mapping.

Flowering may be diurnal (as seen in a majority of taxa) or nocturnal, but in some taxa the distinction between day and night flowering is less evident (Hammer 1993). Pollination itself appears to be non-specialist, relying on moths and pollen wasps for nocturnal and diurnal flowering taxa, respectively (Jürgens & Witt 2014). As such, this would not appear to be a significant limiting factor in the distribution of the genus in south-western Africa. Members of the genus have, however, adapted the timing of flowering to provide a temporal separation from that of the vast majority of other succulents in the region. The bulk of *Conophytum* taxa flower in the late summer to early autumn period, with just a few flowering in spring (e.g. *Conophytum khamiesbergense*) or summer. A recent study has shown the presence of several

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**FIGURE 1:** Typical niche habitats of *Conophytum* in the Succulent Karoo, Fynbos and Desert biomes: (a) *Conophytum pellucidum* ssp. *pellucidum* var. *terricolor* occupying the edges of a shallow grit pan on a granite outcrop in the Namaqualand Klipkoppe Shrubland vegetation unit (SKr1); (b) *Conophytum subterraneum* flowering in quartz gravel in the Kahams Mountain Desert vegetation unit (Dg5); (c) *Conophytum abordellum* ssp. *abordellum* growing on quartzitic sandstone in the Bokkeveld Sandstone Fynbos vegetation unit (FFS1); (d) *Conophytum angelicae* ssp. *tetragonum* growing amongst quartz in the Bushmanland Inselberg Shrubland vegetation unit (SKr18).
discrete pairs of *Conophytum* taxa that lie geographically close to each other (within just 2 km) and in which one taxon flowers in the autumn and the other in the spring (Young et al. 2015).

The aim of this study was to examine the biogeography of members of the genus *Conophytum*, specifically their association with recognised biomes, bioregions and vegetation units in south-western Africa.

**Research method and design**

The database of *Conophytum* locality data (the ‘Conobase’) used to inform this study has been compiled by the authors over several years. The database consists of more than 2,700 individual locality records for the genus, updated to reflect the latest revision of the genus (Hammer & Young in press). Within the database, each taxon was checked for appropriate taxonomic status to subspecies level and nomenclature (updating where appropriate or excluding from the database in cases of uncertainty). Hammer and Young (in press) recognise a total of 165 taxa in the genus *Conophytum* at the species or subspecies level. However, two of these (*Conophytum marschianum* and *Conophytum cupreiflorum*) are natural hybrids and are excluded on that basis. A further five (*Conophytum fibuliforme*, *Conophytum herreanthus* ssp. *herreanthus*, *Conophytum inornatum*, *Conophytum lithopoides* ssp. *boreale* and *Conophytum semivestitum*) are either lost in habitat (possibly extinct) or of uncertain origin. These taxa are therefore also excluded from this analysis. Similarly, we have excluded varieties and any populations of plants for which identification remains uncertain following consultation with photographic records or collections, where available, against standard references (e.g. Hammer 1993, 2002; Hammer & Young in press) and, where appropriate, herbaria records (e.g. the Bolus Herbarium). This includes a number of polyplloid forms, for example, forms of *Conophytum limpidum* on the Bushmanland inselbergs and on the mountains close to the Orange River (Opel 2002).

Locality information was derived primarily from the authors’ (and accompanying colleagues’) direct observations of *Conophytum* taxa in habitat in southern Africa in recent years. Also included are selected records from other recognised experts on the genus (notably Steven Hammer and Anthony Mitchell) where both the identification of the plant and the accuracy of the locality are considered robust or have been confirmed by the authors. GPS records are generally based on centroids. Observations (often historical) in which neither the identity of the plant nor the precise locality (to within an accuracy of ~1 km radius) could be confirmed have been excluded from this study. This has the effect of omitting many of the very earliest observations of members of the genus in habitat.

Distribution analysis and species richness calculations were performed using Cartographica GIS software (Clue Trust Ltd.). The classification of South African Biomes, bioregions and their vegetation types was based on the 2009 update to Vegetation Map of South Africa, Lesotho and Swaziland (Mucina & Rutherford 2006; South African National Biodiversity Institute [SANBI] 2009). For Namibia, the vegetation map of Giess (1971) was used. Shapefiles for conservation areas (formal, informal and focus areas) were also obtained from the SANBI. Both data sets are available from SANBI’s Biodiversity GIS site (http://bgis.sanbi.org). For the purposes of this study, those GPS records that lay very close to a boundary between biomes, bioregions or vegetation units were not adjusted to fit with any particular vegetation type (e.g. at the boundary between the Succulent and Nama Karoo biomes). No records fell on the boundary lines themselves.

**Results**

The distribution of the genus *Conophytum* in southern Africa is shown in Figures 2a and 2b. The vast majority of the 2,798 individual records that comprise the database lie within the western part of the Northern Cape region and the northern extent of the Western Cape of South Africa. By contrast, data records are relatively poor for Namibia. This is primarily a consequence of the restricted access to the Sperregebiet and as a result, the limited number of botanical explorations of this area. The longitudinal range of the genus spans ~800 km from the small Namibian town of Luderitz in the north to Paarl in the Western Cape of South Africa in the south. In contrast, the genus *Conophytum* occupies a fairly narrow latitudinal corridor typically less than 200 km wide, predominantly corresponding to the area that receives winter rainfall. The genus only extends to the east to any significant extent in the northern part of Bushmanland and further south in the Rainshadow Valley Karoo. The northern limit of distribution lies within Namibia in the southern Namib region at the northern limit of the winter-rainfall region, and the genus is not found in the Namib Desert region (see also Hammer 1993). The extent of the genus can also be considered by examining the number of individual locality records per Quarter Degree Square (QDS). This is shown in Figure 3a, and as might be expected, the majority of observed populations lie in those areas with relatively easy access, in the vicinity of towns and near roads or tracks.

The distribution of diurnal and nocturnal flowering taxa is shown in Figures 2a and 2b, respectively. Whilst nearly all areas have examples of both living in close association, within the Rainshadow Valley Karoo bioregion of the Succulent Karoo nocturnal flowering taxa predominate in a majority of vegetation units. The nocturnal flowering extend the range of the genus north to Luderitz in Namibia (*Conophytum saxetanum* and *Conophytum halenbergense*) and south and east to Steytlerville (*Conophytum truncatum*).

Mapping the distribution onto the recognised biomes of the region reveals a very strong association with the Succulent Karoo (Figures 2a and 2b). Almost 83% of all recorded *Conophytum* populations are located solely within this biome (Figure 4). The majority of the remaining observations are found within the Fynbos and Desert biomes, with fewer
recorded populations in the Nama Karoo biome as it is currently geographically defined.

The occurrence of individual taxa (to subspecies level) across all the region’s biomes is shown in Figure 5. Here the close association of the genus with the Succulent Karoo (predominantly in South Africa rather than Namibia) is once again evident with 94% of all recognised Conophytum taxa recorded for this single biome, with 96 separate taxa (i.e. > 60%) endemic to the biome. A number of taxa are found in more than one biome with crossover between the Succulent Karoo and Desert biomes being most pronounced (e.g. Conophytum bilobum ssp. bilobum, Conophytum marginatum ssp. haramoepense and Conophytum lydiae). This is discussed further below. All but eight Conophytum taxa are endemic to South Africa, with the others restricted to south-western Namibia. Just a handful of species (e.g. C. saxetanum, Conophytum loeseliamum and Conophytum angelicae ssp. tetragonum) are found on both sides of the Orange River, sometimes with individual subspecies restricted to just one side of the border, for example Conophytum ernstii ssp. ernstii in South Africa and C. ernstii ssp. cerebellum in Namibia.

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**FIGURE 2:** Distribution of the genus Conophytum in south-western Africa based on the analysis of 2798 locality records in the Conobase: (a) diurnal flowering taxa comprising 116 species and subspecies and (b) nocturnal flowering taxa comprising 42 species and subspecies.

**FIGURE 3:** (a) Conobase sampling intensity (number of Conophytum populations recorded per Quarter Degree Square). (b) Conophytum species richness (Number of Conophytum species and subspecies per Quarter Degree Square).
Taxon richness tends to decline within the Succulent Karoo, the Richtersveld bioregion is host to 67 individual Conophytum taxa including 24 endemic to that bioregion. Within the Richtersveld, species richness is highest within the Kosiesberg Succulent Shrubland (SKr12) and Bushmanland Inselberg Shrubland (SKr18) vegetation units. The Umdaus Mountains Succulent Shrubland (SKr16) is also particularly species rich and an important area for endemism. By contrast, the numbers of both recorded Conophytum taxa and endemics in the Knersvlakte, Namaqualand Sandveld, Rainshadow Valley Karoo and, especially, the Trans-Escarptment Succulent Karoo bioregions are very low (Table 1). In Namibia, a majority of taxa and all Namibian endemics are found within the Desert and Succulent Steppe vegetation zone (see Giess 1971), particularly the Mountain Succulent Dwarf Shrubland vegetation unit.

The incidence of point endemism in the genus is very high, and approximately one fifth of all taxa can be categorised as such (Table 3). The majority of these point endemics (defined here as a contiguous population lacking morphological variation lying within an area of < 10 km²; though areas are typically much smaller) are found in the Succulent Karoo biome (Figure 6). These are severely range-restricted taxa and the area of occupancy for such point endemics can be as small as approximately 1000 m² – 2000 m² (e.g. in the case of Conophytum jarmilae and Conophytum burgeri).

Taxon richness (determined per QDS) is most strongly associated with the Succulent Karoo and especially with the Namaqualand Klipkoppe Shrubland (SKn1) vegetation unit (Figure 3b). Areas on the geographical fringe of this vegetation unit, including the north-western extent of the Bushmanland bioregion of the Nama Karoo and Desert biomes may also show high levels of richness. It is worth noting that even the largest inselbergs in this area may possess no more than one or two taxa (e.g. C. lydiae). Taxon richness tends to decline further south and especially in the south-eastern part of the range of the genus. Here, it is more common to find just one or two taxa per QDS. The area with the highest species diversity for the genus lies around the small Northern Cape town of Steinkopf in the south-eastern Richtersveld (see also Hammer 1993). In the vicinity of this town, it is not uncommon to observe 20 or more individual Conophytum species and subspecies occupying each of several adjacent QDS. Particularly notable for their richness are the quartz hills and gravel plains that can be found on many of the farms to the west of Steinkopf, throughout Umdaus, around Klipbok mine and in the vicinity of the small village of Eksteenfontein.

Nama Karoo Biome

The presence of 30 Conophytum taxa within the Nama Karoo (as determined by mapping onto the latest edition of the VegMap) largely reflects the presence of discrete plant populations close to the boundary with vegetation units of the Succulent Karoo biome. The vast majority of such taxa are found within the Bushmanland Arid Grassland NKh3 vegetation unit in the Bushmanland bioregion. No Conophytum taxa are endemic to the South African Nama Karoo biome, and just one taxon (Conophytum quaesitum ssp. densipunctum) is endemic to the Namibian Nama Karoo biome (Figure 6).
**TABLE 1:** Presence of *Conophytum* taxa (species and subspecies) in the bioregions of South African Biomes.

| Biome    | Bioregion                        | Number of individual taxa | Proportion of total *Conophytum* taxa represented in the bioregion (%) | Number of taxa endemic to the bioregion | Proportion of total *Conophytum* taxa endemic to the bioregion (%) |
|----------|----------------------------------|---------------------------|--------------------------------------------------------------------------|-----------------------------------------|------------------------------------------------------------------|
| Desert   | Gariep Desert                    | 32                        | 20.1                                                                     | 4                                       | 2.5                                                              |
|          | Southern Namib Desert            | 8                         | 5.1                                                                      | 0                                       | 0.0                                                              |
| Fynbos   | East Coast Renosterveld          | 1                         | 0.6                                                                      | 0                                       | 0.0                                                              |
|          | Eastern Fynbos Renosterveld      | 1                         | 0.6                                                                      | 0                                       | 0.0                                                              |
|          | Karoo Renosterveld               | 4                         | 2.5                                                                      | 0                                       | 0.0                                                              |
|          | Namaqualand Cape Shrublands      | 9                         | 5.7                                                                      | 0                                       | 0.0                                                              |
|          | North-west Fynbos                | 11                        | 7.0                                                                      | 3                                       | 1.9                                                              |
|          | South-west Fynbos                | 2                         | 1.3                                                                      | 0                                       | 0.0                                                              |
|          | West Coast Renosterveld          | 2                         | 1.3                                                                      | 0                                       | 0.0                                                              |
|          | West Strandveld                  | 4                         | 2.5                                                                      | 0                                       | 0.0                                                              |
|          | Western Fynbos Renosterveld      | 4                         | 2.5                                                                      | 0                                       | 0.0                                                              |
| Nama Karoo| Bushmanland                      | 22                        | 13.8                                                                     | 0                                       | 0.0                                                              |
|          | Lower Karoo                      | 1                         | 0.6                                                                      | 0                                       | 0.0                                                              |
| Succulent Karoo| Knersvlakte          | 11                        | 6.9                                                                      | 3                                       | 1.9                                                              |
|          | Namaqualand Hardeveld            | 84                        | 53.2                                                                     | 43                                      | 27.0                                                             |
|          | Richtersveld                     | 67                        | 42.4                                                                     | 24                                      | 15.7                                                             |
|          | Namaqualand Sandveld             | 15                        | 9.5                                                                      | 2                                       | 0.0                                                              |
|          | Trans-Escarpment Succulent Karoo | 6                         | 3.8                                                                      | 0                                       | 0.0                                                              |
|          | Rainshadows Valley Karoo          | 10                        | 6.3                                                                      | 4                                       | 2.5                                                              |

**TABLE 2:** Distribution of *Conophytum* taxa (species and subspecies) across individual vegetation units in Southern Africa (taxa are absent from vegetation units not listed here).

| Country     | Bioregion                        | Vegetation unit                        | Number of taxa | Number of taxa endemic to the vegetation unit |
|-------------|----------------------------------|----------------------------------------|----------------|-----------------------------------------------|
| South Africa| Gariep Desert                    | Dg1 Noms Mountain Desert               | 7              | 1                                             |
|             |                                  | Dg2 Richtersberg Mountain Desert       | 1              | 0                                             |
|             |                                  | Dg3 Richtersberg Sheet Wash Desert     | 1              | 0                                             |
|             |                                  | Dg5 Kahams Mountain Desert             | 10             | 2                                             |
|             |                                  | Dg6 Helskloof Canyon Desert            | 3              | 0                                             |
|             |                                  | Dg7 Northern Nabhiepsberge Mountain Desert| 2              | 0                                             |
|             |                                  | Dg8 Southern Nabhiepsberge Mountain Desert| 11            | 0                                             |
|             |                                  | Dg9 Eastern Gariep Plains Desert       | 1              | 0                                             |
|             |                                  | Dg10 Eastern Gariep Rocky Desert       | 17             | 1                                             |
|             |                                  | Dn3 Western Gariep Plains Desert       | 1              | 0                                             |
|             |                                  | Dn4 Western Gariep Lawlow Desert       | 1              | 0                                             |
|             |                                  | Dn5 Western Gariep Hills Desert        | 7              | 0                                             |
|             | Bushmanland                      | NKB3 Bushmanland Arid Grassland        | 22             | 0                                             |
|             |                                  | NKB4 Bushmanland Sandy Grassland       | 2              | 0                                             |
| Lower Karoo |                                  | NKB1 Gamka Karoo                      | 1              | 0                                             |
| East Coast Renosterveld | FRs8 Breede Shale Renosterveld | 1                      | 0 | 0 |
| Fynbos      | Eastern Fynbos Renosterveld      | FFs28 Kouga Grassy Sandstone Fynbos    | 2              | 0                                             |
|             | Karoo Renosterveld               | FRs24 Hantam Plateau Dolerite Renosterveld | 1              | 0                                             |
|             | Namaqualand Cape Shrublands      | FFs1 Vanrhynsdorp Shale Renosterveld   | 3              | 0                                             |
|             |                                  | FRs2 Nieuwoudville Shale Renosterveld  | 3              | 0                                             |
|             | Namaqualand Sandveld             | FFg1 Kamiesberg Granite Fynbos         | 1              | 0                                             |
|             |                                  | FFq1 Stinkfonteinberge Quartzite Fynbos| 1              | 1                                             |
|             |                                  | FRg1 Namaqualand Granite Renosterveld  | 8              | 0                                             |
| North-west Fynbos | FFb1 Northern Inland Shale Band Vegetation | 2 | 0 | |
|             |                                  | FFb2 Leipoldtville Sand Fynbos         | 2              | 0                                             |
|             |                                  | FFs1 Bokkevel Sandstone Fynbos         | 8              | 2                                             |
|             |                                  | FFs2 Graafwater Sandstone Fynbos       | 5              | 0                                             |
|             |                                  | FFs3 Olifants Sandstone Fynbos         | 1              | 0                                             |
|             |                                  | FFs4 Cederberg Sandstone Fynbos        | 3              | 0                                             |
|             |                                  | FFs6 Piketberg Sandstone Fynbos        | 1              | 0                                             |
|             |                                  | FFq2 Swartruggens Quartzite Fynbos     | 3              | 0                                             |
| South-west Fynbos | FFd2 Leipoldtville Sand Fynbos | 2 | 0 | |
|             |                                  | FFs1 Bokkevel Sandstone Fynbos         | 8              | 2                                             |
|             |                                  | FFs2 Graafwater Sandstone Fynbos       | 5              | 0                                             |
| West Coast Renosterveld | FRs24 Hantam Plateau Dolerite Renosterveld | 1 | 0 | |
| West Strandveld | FS1 Lambert’s Bay Sand | 3 | 0 | |
|             |                                  | FS2 Saldanha Granite Sandveld          | 1              | 0                                             |

Table 2 continues on the next page
### TABLE 2 (Continues...): Distribution of Conophytum taxa (species and subspecies) across individual vegetation units in Southern Africa (taxa are absent from vegetation units not listed here).

| Country            | Bioregion          | Vegetation unit                                      | Number of taxa | Number of taxa endemic to the vegetation unit |
|--------------------|--------------------|-----------------------------------------------------|----------------|-----------------------------------------------|
| Western Fynbos     | Renosterveld       | FFq3 Matjiesfontein Quartzite Fynbos                | 2              | 0                                             |
|                    |                    | FFs23 North Swartberg Sandstone Fynbos              | 1              | 0                                             |
|                    |                    | FFs32 Nardouw Sandstone Fynbos                      | 3              | 0                                             |
|                    |                    | FR6 Matjiesfontein Shale Renosterveld              | 1              | 0                                             |
| Knersvlakte        |                    | SKk1 Northern Knersvlakte Vygieveld                | 4              | 0                                             |
|                    |                    | SKk2 Central Knersvlakte Vygieveld                 | 5              | 0                                             |
|                    |                    | SKk3 Knersvlakte Quartz Vygieveld                  | 8              | 1                                             |
|                    |                    | SKk4 Knersvlakte Shale Vygieveld                   | 3              | 0                                             |
|                    |                    | SKk5 Vanrhynsdorp Gannabosveld                     | 4              | 0                                             |
|                    |                    | SKk6 Knersvlakte Dolomite Vygieveld                | 1              | 0                                             |
|                    |                    | SKk7 Citrusdal Vygieveld                           | 3              | 0                                             |
|                    |                    | SKk9 Kobee Succulent Shrubland                     | 2              | 0                                             |
|                    | Namaqualand        | SKn1 Namaqualand Klipkoppie Shrubland              | 67             | 23                                            |
|                    | Hardeveld          | SKn2 Namaqualand Shale Shrubland                   | 13             | 2                                             |
|                    |                    | SKn3 Namaqualand Blomveld                          | 34             | 4                                             |
|                    |                    | SKn4 Namaqualand Heuweltjieveld                    | 13             | 2                                             |
|                    |                    | SKn5 Platbakkies Succulent Shrubland               | 12             | 3                                             |
|                    |                    | SKn6 Kamiesberg Mountains Shrubland                | 1              | 0                                             |
|                    | Richtersveld       | SKr1 Central Richtersveld Mountain Shrubland       | 13             | 1                                             |
|                    |                    | SKr3 Goariep Mountain Succulent Shrubland          | 4              | 1                                             |
|                    |                    | SKr4 Lekkersing Succulent Shrubland                | 12             | 1                                             |
|                    |                    | SKr5 Vytiennyl se Berge Succulent Shrubland       | 10             | 3                                             |
|                    |                    | SKr6 Stinkfonteinberge Eastern Apron Shrubland     | 5              | 0                                             |
|                    |                    | SKr7 Northern Richtersveld Scorpionstailveld      | 2              | 0                                             |
|                    |                    | SKr8 Rosyntjieberg Succulent Shrubland             | 3              | 0                                             |
|                    |                    | SKr9 Tataseberg Mountain Succulent Shrubland       | 1              | 0                                             |
|                    |                    | SKr10 Die Plate Succulent Shrubland                | 5              | 0                                             |
|                    |                    | SKr11 Rooberg Quartz Vygieveld                     | 8              | 0                                             |
|                    |                    | SKr12 Kosiesberg Succulent Shrubland               | 25             | 2                                             |
|                    |                    | SKr13 Southern Richtersveld Scorpionstailveld     | 7              | 0                                             |
|                    |                    | SKr14 Southern Richtersveld Inselberg Shrubland    | 11             | 1                                             |
|                    |                    | SKr15 Anenous Plateau Shrubland                    | 12             | 1                                             |
|                    |                    | SKr16 Umdaua Mountains Succulent Shrubland         | 18             | 3                                             |
|                    |                    | SKr17 Eenriet Plains Succulent Shrubland           | 9              | 0                                             |
|                    |                    | SKr18 Bushmanland Inselberg Shrubland              | 23             | 3                                             |
| Namaqualand        | Sandveld           | SKs1 Richtersveld Coastal Dunveled                 | 1              | 0                                             |
|                    |                    | SKs7 Namaqualand Strandveld                        | 13             | 0                                             |
|                    |                    | SKs8 Namaqualand Coastal Dunveled                  | 1              | 0                                             |
|                    |                    | SKs10 Riethuis-Wallekraal Quartz Vygieveld         | 6              | 0                                             |
|                    |                    | SKs11 Namaqualand Arid Grassland                   | 4              | 0                                             |
|                    | Trans-Escarpment   | SKt1 Western Bushmanland Klipveld                  | 1              | 0                                             |
| Karoo              |                    | SKt2 Hantam Karoo                                  | 5              | 0                                             |
|                    | Rainshadow Valley  | SKv1 Doringrivier Quartzite Karoo                  | 2              | 0                                             |
| Karoo              |                    | SKv2 Swartruggens Quartzite Karoo                  | 2              | 0                                             |
|                    |                    | SKv3 Agter-Sederberg Shrubland                     | 1              | 0                                             |
|                    |                    | SKv5 Tanqua Karoo                                  | 3              | 0                                             |
|                    |                    | SKv6 Koedoesberge-Moordenaars Karoo                | 1              | 0                                             |
|                    |                    | SKv7 Robertson Karoo                               | 1              | 0                                             |
|                    |                    | SKv8 Western Little Karoo                          | 4              | 1                                             |
|                    |                    | SKv9 Western Gwarrieveld                           | 2              | 0                                             |
|                    |                    | SKv10 Little Karoo Quartz Vygieveld                | 2              | 1                                             |
|                    |                    | SKv14 Steytlerville Karoo                          | 1              | 0                                             |
| Namibia             | Dwarf Shrub        | DS-1 Karas Dwarf Shrubland                          | 4              | 0                                             |
| Savannah           |                    | DST-2 Desert/Dwarf Shrub Transiton                 | 4              | 0                                             |
|                    | Desert and Succulent Steppe                           | SS-1 Plain Dwarf Shrubland                         | 1              | 0                                             |
|                    |                    | SS-2 Mountain Succulent Dwarf Shrubland            | 11             | 6                                             |
|                    |                    | SS-3 Sand Plain Succulent Dwarf Shrubland          | 1              | 0                                             |

Note: The vegetation zones for Namibia were defined by Giess, W., 1971, ‘A preliminary vegetation map of South West Africa’, Dinteria 4, 5–14.
### TABLE 3: Conophytum taxa (species and subspecies) endemic to Biomes in South Africa and Namibia.

| Biome              | Species and subspecies                                                                 |
|--------------------|----------------------------------------------------------------------------------------|
| **Desert Biome**   | C. cubicum†                                                                            |
|                    | C. ernstii ssp. ernstii                                                                |
|                    | C. jucundum ssp. jucundum                                                              |
|                    | C. jucundum ssp. marlothii                                                             |
|                    | C. jucundum ssp. ruschi                                                               |
|                    | C. lithaspides ssp. koubergense†                                                       |
|                    | C. longibracteatum†                                                                     |
|                    | C. maughani ssp. armeniacum                                                             |
|                    | C. maughani ssp. latum                                                                 |
|                    | C. meyeri                                                                              |
|                    | C. mirabile†                                                                          |
|                    | C. obcordellum ssp. stenandrum                                                        |
|                    | C. obscurum ssp. barbatum†                                                             |
|                    | C. obscurum ssp. spongisaurorum                                                        |
|                    | C. obscurum ssp. vitreopapillum†                                                       |
|                    | C. pellicium ssp. cupreatum                                                             |
|                    | C. pellicium ssp. saueri†                                                               |
|                    | C. phoeniceum                                                                          |
|                    | C. piuliforme ssp. piuliforme                                                          |
|                    | C. piuliforme ssp. edwardii                                                           |
|                    | C. piuliforme ssp. regale†                                                             |
|                    | C. raadiae ssp. rodiae                                                                  |
|                    | C. raadiae ssp. corrugatum                                                             |
|                    | C. raadiae ssp. sanguineum†                                                            |
|                    | C. schlechteri†                                                                        |
|                    | C. smoreskadhunense†                                                                   |
|                    | C. stephanii ssp. stephanii†                                                           |
|                    | C. subfenestratum                                                                     |
|                    | C. tantillum ssp. amicorum†                                                            |
|                    | C. tantillum ssp. helenia†                                                             |
|                    | C. tantillum ssp. inexpectatum†                                                        |
|                    | C. tantillum ssp. lindenianum                                                          |
|                    | C. tantillum ssp. tantillum                                                            |
|                    | C. taylorianum ssp. rosynsense                                                        |
|                    | C. untormiforme ssp. decoratum                                                         |
|                    | C. untormiforme ssp. rauhi                                                             |
|                    | C. untormiforme ssp. subincanum†                                                       |
|                    | C. vanheerdei†                                                                         |
|                    | C. velutinum ssp. velutinum                                                              |
|                    | C. velutinum ssp. polyanthrum                                                           |
|                    | C. verrucosum                                                                          |
|                    | C. violasciflorum                                                                     |
|                    | C. wettsteinii                                                                         |
|                    | C. youngii†                                                                            |
|                    | C. zonale                                                                              |

**Note:** Point endemics are marked (†) and are defined here as a contiguous population lacking morphological variation lying within an area < 10 km². See also Figure 3 for the distribution of point endemics.

### Desert Biome

The Desert biome possesses only a fifth the number of taxa of the Succulent Karoo, with 33 taxa present, of which 21% are endemic to the biome (Figure 3). The most important vegetation units are the Kahamas Mountain Desert Dg5, Southern Nababiepsberge Mountain Desert Dg8 and especially the Eastern Gariep Rocky Desert Dg10 (Table 4).
Informal protected areas

| Number of taxa | C. comptonii | 10 |

The level of endemism within each region varies, with the Succulent Karoo biome having the highest level of endemism (33–59%) among the bioregions. The Fynbos biome has a lower level of endemism, with the majority of taxa found in the north-west Fynbos bioregion and the remaining taxa distributed across the biome and present in 9 of the 12 bioregions.

Other transition zones include the Richtersveld, Hantam-Tanqua-Roggeveld, and Namib Desert regions. The Richtersveld centre is separated out from the other GCFR centres, with eight taxa found in each unit. These taxa are also primarily restricted to the western extent of the region where winter-rainfall conditions prevail. Overall, the region has surprisingly few taxa (22) and the genus is absent from the Karoo centre.

The Hantam-Tanqua-Roggeveld region has only three Conophytum taxa (all nocturnal), none of which are endemic to the region. These taxa are also primarily restricted to the western extent of the region where winter-rainfall conditions prevail. The Namib Desert region has four taxa, all of which are endemic to the region. The mapping of the distribution of the genus onto the centres of the Greater Cape Floristic Region provides a further interpretation of the distribution of the genus and its relationship to other floras.

Mapping the distribution of the genus onto the centres of the Greater Cape Floristic Region, as defined by Born, Linder & Desmet (2007), shows that the Succulent Karoo biome is the richest, with eight taxa present in each unit. The Veld biome has the second highest level of endemism, with six taxa present in each unit.

The distribution of taxa within the GCFR is very high (33%–59%), reflective of a high degree of habitat specialism.

Fynbos Biome

Conophytum is relatively poorly represented in the Fynbos biome, with only 27 taxa present, of which 7 (26%) are endemics (Table 3). Members of the genus are widely distributed across the biome and are present in 9 of the 12 bioregions and in 26 vegetation units, but typically with only 1 to 3 taxa found in each unit. The Bokkeveld Sandstone Fynbos FFs1 and Namaqualand Granite Renosterveld FRg1 units are the richest, with eight taxa found in each unit (Table 4). Three of the taxa endemic to this biome are found in the north-west Fynbos bioregion, and the remaining taxa are found in at least two bioregions (Tables 1 and 2).

Greater Cape Floristic Region

Mapping the distribution of the genus onto the centres of the Greater Cape Floristic Region (as defined by Born, Linder & Desmet 2007) provides a further interpretation of the distribution of the genus and its relationship to other floras (Table 5). Because of the importance of the Richtersveld to Conophytum, this centre is separated out from the other rainfall transition centres. The vast majority of taxa are found within the Richtersveld centre and the Namaqualand region. By contrast, the Hantam-Tanqua-Roggeveld region has only three Conophytum taxa (all nocturnal), none of which are endemic to the region. These taxa are also primarily restricted to the western extent of the region where winter-rainfall conditions prevail. Overall, the region has surprisingly few taxa (22) and the genus is absent from the Karoo centre.

The Hantam-Tanqua-Roggeveld region has only three Conophytum taxa (all nocturnal), none of which are endemic to the region. These taxa are also primarily restricted to the western extent of the region where winter-rainfall conditions prevail. Overall, the region has surprisingly few taxa (22) and the genus is absent from the Karoo centre.

TABLE 4: South African Conophytum taxa (species and subspecies) that currently lie within the boundaries of existing formal and informal protected areas.

| Formal protected areas | Informal protected areas |
|------------------------|--------------------------|
| C. angeliacae ssp. tetragonum | C. albiflorum |
| C. bilobum ssp. bilobum | C. comptonii |
| C. bolusiae ssp. bolusiae | C. minusculus ssp. aestiflorens |
| C. breve | C. minusculus ssp. minusculus |
| C. calculus ssp. calculus | C. acordellium ssp. acordellium (var. cerasianum) |
| C. calculus ssp. vanzylii | C. piluliforme ssp. edwardii |
| C. carpinum | |
| C. cubicum† | |
| C. depressum ssp. depressum | |
| C. ernstii ssp. ernstii | |
| C. francoisae† | |
| C. fraternum | |
| C. hians | |
| C. jouberti | |
| C. jucundum ssp. fragile | |
| C. jucundum ssp. marlothii | |
| C. jucundum ssp. ruschii | |
| C. loechianum | |
| C. luckhoffii | |
| C. meyeri | |
| C. minimum | |
| C. minusculus ssp. minusculus | |
| C. minutum | |
| C. obscurum ssp. obscurum | |
| C. obscurum ssp. barbarum† | |
| C. obscurum ssp. vitreapapullum† | |
| C. pageae | |
| C. pellucidum ssp. pellucidum | |
| C. piluliforme ssp. piluliforme | |
| C. quaesitum ssp. rastratum | |
| C. rodliae ssp. rodliae | |
| C. rodliae ssp. corrugatum | |
| C. stephani ssp. stephani† | |
| C. stephani ssp. helmuthii | |
| C. stevens-jonesianum | |
| C. subfenestratum | |
| C. subterranean† | |
| C. taylorianum ssp. rosynense | |
| C. truncatum ssp. truncatum | |
| C. turneri | |
| C. uviforme ssp. uviforme | |
| C. uviforme ssp. decoratum | |
| C. uviforme ssp. subincanum† | |
| C. wettsteinii | |
| C. wettsteinii | |

Note: Point endemics are defined here as a contiguous population lacking morphological variation lying within an area < 10 km². The Succulent Karoo biome is shaded.
Conservation

The conservation status of members of the genus has been examined for formal and informal protected areas, as well as focus areas identified by the South African National Protected Areas Expansion Strategy (NPAES). Currently, 47 taxa (including 36 species) lie within formal protected areas, representing ~30% of the genus (Table 4). In addition, a further six taxa are found within informal protected areas, of which three are not already protected. When combined, such areas in South Africa provide protection for 50 separate Conophytum species and subspecies. The NPAES focus areas have the potential to extend protection to a further 76 taxa and provide additional area for 30 protected taxa. Within Namibia, all endemic Conophytum taxa, with the exception of C. quaesitum ssp. densipunctum, can be found within or are restricted to existing protected areas, namely the Sperrgebiet National Park and the Ai-Ais Richtersveld Transfrontier National Park.

Discussion

With almost 3000 records, the Conobase currently provides the most up-to-date, comprehensive and accurate record of distribution of members of the dwarf succulent genus Conophytum. In compiling this data set, a large number of records have been excluded where there were uncertainties concerning the accuracy of the locality data (a particular problem with older herbaria records, e.g. those held at the Bolus, Compton or Kew herbaria) or with their taxonomic identification (e.g. with dried samples). Nevertheless, there are limitations associated with its use, including (1) sampling bias towards Namaqualand and away from either Namibia (in part because of access restrictions) or the south-eastern extent of the genus’ distribution; (2) challenges in successfully identifying taxa to subspecies level within some species (e.g. C. jucundum), and even the separation of some species (especially with the taxa that comprise section Ophthalmophyllum) and (3) large-scale vegetation mapping exercises such as the South African VegMap do not always successfully capture the presence of localised or very small populations of plants (e.g. on discrete rocky outcrops such as those favoured by some Conophytum taxa) with the result that some of the point locality data used here may not always align well with boundaries between biomes (a particular issue with the boundary between Succulent Karoo and Nama Karoo biomes in this study). This is discussed in more detail below.

The distribution of the genus Conophytum is closely associated with the winter-rainfall region of southern Africa, and especially the Succulent Karoo biome (Figure 2a and 2b). The influence of environmental factors governing the distribution of the genus in the region will be analysed in more detail in a further study. Rainfall levels across the Karoo diminish from south to north and from east to west (Desmet & Cowling 1999b) and rainfall, together with significant local influences of fog and dew, is a major factor in influencing both the distribution and richness of flora across the region.

The influence of precipitation cannot be viewed in isolation and the importance of seasonal temperatures is also a significant factor in determining the distribution of the genus Conophytum (Young et al. 2016).

Within the Greater Cape Floristic Region, high levels of Conophytum taxon richness and endemism prevail in just a few centres, notably Springbok, Kamiesberg, Richtersveld and, to a lesser extent, the Knersvlakte (see below). This pattern generally correlates with the observations of Born et al. (2007) concerning the wider flora of the region. However, whilst the Namaqualand and Hantam-Tanqua-Roggeveld centres are floristically similar (Born et al. 2007), the genus Conophytum is almost completely absent from the latter (where members of the Aizoaceae are generally well represented). Conophytum is completely absent from the predominantly summer-rainfall Karoo centre. Surprisingly, fewer than 15% of taxa are found within the Cape Floristic Region itself (Table 5), with the amount of rainfall rather than its seasonality thought to be a limiting factor. Overall, many Conophytum can be considered to be habitat specialists, well adapted to the prevailing environmental conditions as seen, for example, in those taxa occupying the Namib-Desert region.

When examined at the biome level, it is clear that the Succulent Karoo possesses the highest degree of taxon richness for the genus (c.f. Figures 3a and 3b). A recognised global biodiversity hot spot and one of only two entirely arid hotspots (Cowling et al. 1998; Mittermeier et al. 2004), the biome is characterised by a high degree of floral endemism, especially in dwarf-leaf succulents (Driver et al. 2003; Mucina et al. 2006a). Both taxon richness and endemism of Conophytum within the Namaqualand Hardeveld bioregion are consistent with the pattern seen in the flora as a whole (Snijman 2013). However, the level of Conophytum endemism in the Knersvlakte bioregion is low by comparison to that seen in other plants.

More than 93% of Conophytum taxa are recorded in the Succulent Karoo biome, with many of the remaining taxa located on the biome’s immediate fringes and often in the transitional area at the boundary of winter- and summer-rainfall areas. The propensity towards endemism, which is reflective of the extent of speciation in this genus, is also a strong characteristic, with ~60% of all Conophytum taxa endemic to this biome. Most of the biome is characterised by low and rather unpredictable levels of rainfall in the winter months, and it is in these parts of the biome that the genus predominates. Conophytum is much less common, and may be absent, in the eastern parts of the biome that experience year-round or bimodal rainfall patterns (e.g. in the Trans-Escarpment Succulent Karoo and the Rainshadow Valley Karoo; (Bradshaw & Cowling 2014)).

Normalising the data shown in Table 2 to account for differences in the areas occupied by individual vegetation units serves to identify four units with very high taxon richness per unit area: Dg6 Helskloof Canyon Desert, Skr5
Conophytum (especially that between the Succulent and Nama Karoo), Desert, Nama Karoo, Fynbos and Thicket biomes. Whilst the Succulent Karoo shares boundaries with the Desert biome, the genus is most prevalent and is well distributed across both the Namaqualand Hardeveld and Northern Nama Karoo bioregions (Rebelo et al. 2016). The vast majority of records in the Conobase arise from South Africa, whilst data for Namibia remains poor. Despite this, all the taxa known to Namibia are recorded: 15 in total, including six endemic to the country. Within Namibia, Conophytum taxa are once again primarily found in the Succulent Karoo (within the Desert and Succulent Steppe vegetation zone; Giess 1971), as is the case south of the Orange River. Within South Africa, the genus is most prevalent and is well distributed across both theNamaqualand Hardeveld and Richtersveld bioregions (Table 1). Geology plays a very significant part in the distribution of the genus with separate taxa showing distinct preferences for sandstone, granite, gneiss and especially quartz (Hammer 1993; Young et al. 2016). The Succulent Karoo shares boundaries with the Desert, Nama Karoo, Fynbos and Thicket biomes. Whilst the transition from one biome to the next is often unclear (especially that between the Succulent and Nama Karoo), Conophytum taxa are found in all but the Thicket biome (Table 1). It is interesting to note that none of the taxa that have been discovered over the past 10–15 years have extended the known geographical range of the genus. Instead, new taxa have been found in close proximity to other Conophytum populations, often in areas of existing high biodiversity in the Succulent Karoo (e.g. Conophytum smealeorum in the southern Richtersveld).

Equally low, rainfall as in the Succulent Karoo, but with much greater variability and oriented to a summer phenological peak characterise the Nama Karoo (1999b), resulting in very low diversity and abundance of succulents; Mucina et al. (2006b). The Nama Karoo is not especially florally rich and local endemism is relatively poor compared to other biomes (Cowling et al. 1998; Mucina et al. 2006b; Van Wyk & Smith 2001). This is reflected in the genus Conophytum with just a few taxa and only a single endemic (in Namibia) present in this biome. The occurrence of Conophytum in the Nama Karoo is always in association with habitats or vegetation types that are still under the influence of the winter-rainfall systems. This is especially prevalent in the Bushmanland Inselberg Region where the topography supports isolated outliers of Succulent Karoo vegetation units. Nearly all taxa are found in Bushmanland Arid Grassland (NKb3), but such instances are nearly always on the fringes of the Succulent Karoo itself, often within a few hundred metres of the boundary between the biomes. A good example of a taxon that could be considered endemic to the Succulent Karoo is Conophytum ratum but strict application of the VegMap also situates it in the Nama Karoo. Such examples highlight some of the limitations in using the VegMap to analyse such point data but would also support the need to further refine the biome and vegetation unit boundaries on the VegMap to aid conservation planning.

The Desert biome occupies an area along the Atlantic Coast and the Orange River. By contrast with the Succulent Karoo, this biome generally affords rather sparse vegetation cover. Rainfall is highly variable and shows marked west-east transition (Jürgens 2006). Similarly, temperatures are often very variable, and extremely high. Here fog can play a key role as a critical source of moisture and it is along the Orange River and the mountainous desert section of the Richtersveld region with exposure to winter rainfall and coastal fog that floral endemism is most prevalent (Jürgens 1991, 1997). This is similarly reflected in the distribution of the genus Conophytum (Tables 1 and 2). Bordering the Succulent Karoo to the south and south-west, the Fynbos biome is host to surprisingly few Conophytum taxa, with just seven endemic to the biome (Figure 5 and Table 3). This contrasts with the overall species richness of the biome, especially the Renosterveld vegetation complex (Rebelo et al. 2006). Winter rainfall is most prevalent in the western part of the Cape region, where the majority of taxa are found. In common with all other biomes, geology is a major factor in plant distribution with sandstone and quartz playing a key role in creating Conophytum habitat (Hammer 1993; Young et al. 2016).
A strong feature of the genus is its geographical fragmentation into spatially isolated taxa, often with a highly restricted distribution: almost one quarter of all Conophytum taxa are known from only a single locality. Such localities may include single mountains (e.g. Conophytum cubicum on Black Face Mountain), Bushmanland inselbergs (e.g. Conophytum achabense on Achab), small hills (e.g. Conophytum schlecteri on Farquarson-se-kop), quartz ridges (e.g. Conophytum regale north of Springbok) or quartz gravel flats (e.g. C. burgeri at Aggeneys). Whilst the geographical range of the majority of taxa is generally restricted, a few species, such as C. bilobum, Conophytum jucundum, Conophytum pellucidum and Conophytum pageae, have a longitudinal range of hundreds of kilometres. Most notable amongst these is C. pageae, which is one of a handful of taxa to be found in both Namibia and South Africa, with a range extending from the small town of Garies in the Northern Cape to the Sperrgebiet Namibia and South Africa, with a range extending from the Namaqualand especially around the towns of Steinkopf and Springbok offer some of the greatest potential for conservation purposes. Such areas are, at least partially, already identified as NPAES focus areas (see also Driver et al. 2003). Even in a scenario that would see all formal, informal and NPAES focus areas in place, approximately one quarter of all Conophytum taxa (including some vulnerable point endemics, including Conophytum bolusiae ssp. primaverrum) would lie outside any protection. Given the level of regional endemism, especially point endemism, within the genus as a whole this is a concern. The Conobase now provides a tool to inform such matters by initially identifying those taxa at potential risk. The data have most recently informed the South African Red List in which approximately 50% of Conophytum taxa (including recognised varieties) are now provisionally categorised as threatened, critically rare or rare (South African National Biodiversity Institute 2015).

One of the questions that this study sought to explore was whether the genus Conophytum could be employed as a model dwarf succulent taxon for the Succulent Karoo biome. The data here show that the genus has a strong association with this particular biome and many of its bioregions and vegetation units, with taxa found in all but 14 of the 63 vegetation units currently recognised by the 2009 vegetation map, including all six of the Namaqualand Hardeveld bioregion and 18 of 19 that comprise the Richtersveld bioregion. However, the association is weaker in the Rainshadow Valley Karoo (10 of 14 vegetation units) and Namaqualand Sandveld (5 of 13 units) bioregions and, in the latter, is generally restricted to isolated, often small, rocky outcrops.

Conclusion

The genus Conophytum displays a strong affinity with the Succulent Karoo biome, that is, that component of the arid ecotone between winter- and summer-rainfall regimens in south-western Africa that demonstrates a strong winter phenological peak. Members of the genus are found in a majority but not all vegetation units of the biome, with taxon richness and endemism highest in those units falling within the Namaqualand Hardeveld and Richtersveld bioregions.

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Competing interests

The authors declare that they have no financial or personal relationships which may have inappropriately influenced them in writing this article.

Authors’ contributions

Both A.J.Y. and P.G.D. were jointly responsible for the design of the study, compiled the locality database used in this study and co-wrote the article. A.J.Y. performed the analyses.
References

Born, J., Linder, H.P. & Desmet, P., 2007, ‘The Greater Cape Floristic Region’, Journal of Biogeography 34, 147–162.

Bradshaw, P.L. & Cowling, R.M., 2014, ‘Landscapes, rock types, and climate of the Greater Cape Floristic Region’, in N. Alliopp, J.F. Colville & A.A. Verboom (eds.), Fynbos: Ecology, evolution, and conservation of a Megadiverse Region, pp. 26–47, Oxford University Press, Oxford.

Cowling, R.M. & Hilton-Taylor, C., 1994, ‘Phytogeography. Flora and endemism’, in R.M. Cowling, D.M. Richardson & S.M. Pierce (eds.), Vegetation of Southern Africa, pp. 3–61, Cambridge University Press, Cambridge.

Cowling, R.M. & Hilton-Taylor, C., 1999, ‘Plant biogeography, endemism and diversity’, in W.R.J. Dean & S. Milton (eds.), The Karoo. Ecological patterns and processes, pp. 42–56, Cambridge University Press, Cambridge.

Cowling, R.M., Rundel, P.W., Desmet, P.G. & Esler, K.J., 1998, ‘Extraordinary high regional-scale plant diversity in southern African arid lands: Subcontinental and global comparisons’, Diversity and Distributions 4, 27–36.

Desmet, P. & Cowling, R., 1999a, ‘Biodiversity, habitat and range-size aspects of a flora from a winter-rainfall desert in north-western Namaqualand, South Africa’, Plant Ecology 142, 23–33.

Desmet, P. & Cowling, R., 1999b, ‘The climate of the karoo. A functional approach’, in W.R.J. Dean & S. Milton (eds.), The Karoo. Ecological patterns and processes, pp. 3–16, Cambridge University Press, Cambridge.

Desmet, P.G., Ellis, A.G. & Cowling, R.M., 1998, ‘Speciation in the Mesembryanthemaceae’, Aloe 35, 38–43.

Driver, A., Desmet, P., Rouget, M., Cowling, R. & Maze, K., 2003, Succulent Karoo ecosystem plan: Biodiversity component, Cape Conservation Unit Technical Report, Cape Town.

Giess, W., 1971, ‘A preliminary vegetation map of South West Africa’, Dinteria 4, 5–14.

Hammer, S.A., 1993, The genus Conophytum: A conograph, Succulent Plant Publications, Pretoria.

Hammer, S.A., 2002, Dumpling and his wife: New views on the genus Conophytum, EAE Creative Colour Ltd, Norwich.

Hammer, S.A. & Young, A.J., in press, ‘Conophytum: Ruschioidae’, in H.E.K. Hartman, (ed.), illustrated handbook of succulent plants, Springer-Verlag, Heidelberg.

Hilton-Taylor, C., 1996, ‘Patterns and characteristics of the flora of the Succulent Karoo Biome in southern Africa’, in L.J.E. Van der Maesen, X.M. Van der Burgt & I.M. Van Medenbach de Rooy (eds.), The biodiversity of African plants, pp. 58–72, Kluwer Academic Publishers, Dordrecht.

Ihlenfeldt, H.-D., 1994, ‘Diversification in an arid world: The mesembryanthemaceae’, Annual Review of Ecology and Systematics 25, 521–546.

Jürgens, N., 1991, ‘A new approach to the Namib Region. I. Phytogeographic subdivision’, Vegetation 97, 21–38.

Jürgens, N., 1997, ‘Floristic biodiversity and history of African arid regions’, Biodiversity and Conservation 6, 495–514.

Jürgens, N., 2006, ‘Desert Biome’, in L. Mucina & M.C. Rutherford (eds.), The vegetation of South Africa, Lesotho and Swaziland, Strelitzia 19, pp. 301–323, South African National Biodiversity Institute, Pretoria.

Jürgens, A. & Witt, T., 2014, ‘Pollen-oval ratios and flower visitors of day-flowering and night-flowering Conophytum (Aizoaceae) species in South Africa’, Journal of Arid Environments 109, 44–53.

Matimati, I., Musi, C.F., Raitt, L. & February, E., 2012, ‘Non rainfall moisture interception by dwarf succulents and their relative abundance in an inland arid South African ecosystem’, Ecohydrology 6, 819–825.

Mittermeier, R.A., Robles Gil, P., Hoffman, M., Pilgrim, J., Brooks, T., Goettsch Mittermeier, C. et al., 2004, Hotspots revisited: Earth’s biologically richest and most endangered terrestrial ecoregions, Conservation International & CEMEX. P. 392, Mexico City.

Mucina, L., Jürgens, N., Le Roux, A., Rutherford, M.C., Schmiedel, U., Esler, K. et al., 2006a, ‘Succulent Karoo Biome’, in L. Mucina & M.C. Rutherford (eds.), The vegetation of South Africa, Lesotho and Swaziland, Strelitzia 19, pp. 221–299, South African National Biodiversity Institute, Pretoria.

Mucina, L. & Rutherford, M.C. (eds.), 2006, The vegetation of South Africa, Lesotho and Swaziland, Strelitzia 19, South African National Biodiversity Institute, Pretoria.

Mucina, L., Rutherford, M.C., Palmer, A.R., Milton, S.J., Scott, L., Lloyd, W. et al., 2006b, ‘Nama-Karoo Biome’, in L. Mucina & M.C. Rutherford (eds.), The vegetation of South Africa, Lesotho and Swaziland, Strelitzia 19, pp. 221–299, South African National Biodiversity Institute, Pretoria.

Opel, M.R., 2002, ‘Chromosome numbers of Conophytum and related genera’, in S.A. Hammer (ed.), Dumpling and his wife: New views on the genus Conophytum, pp. 332–340, EAE Creative Colour Ltd, Norwich.

Rebelo, A.G., Boucher, C., Helme, N., Mucina, L. & Rutherford, M.C. 2006, ‘Fynbos Biome’, in L. Mucina & M.C. Rutherford (eds.), The vegetation of South Africa, Lesotho and Swaziland, Strelitzia 19, pp. 53–219, South African National Biodiversity Institute, Pretoria.

Snijman, D.A., 2013, ‘The Greater Cape Floristic Region: The Extra Cape Subregion’, in D.A. Snijman (ed.), Plants of the Greater Cape Floristic Region, The Extra Cape Flora, Strelitzia 30, Vol. 2, pp. 1–23, South African National Biodiversity Institute, Pretoria.

South African National Biodiversity Institute, 2009, Vegetation map of South Africa, Lesotho and Swaziland 2009, viewed 09 November 2015, from http://www.bgsb.nbi.org

South African National Biodiversity Institute, 2015, Red list of South African plants, viewed from http://redlist.sanbi.org. 14/12/2015.

Van Wyk, A.E. & Smith, G.F., 2001, Regions of floristic endemism in southern Africa: A review with emphasis on succulents, Umdaus Press, Pretoria.

Young, A.J., Guo, D., Desmet, P.G. & Midgley, G.F., 2016, ‘Biodiversity and climate change: Risks to dwarf succulents in Southern Africa’, Journal of Arid Environments 129, 16–24.

Young, A.J., Rodgerson, C., Opel, M.R. & Hammer, S.A., 2015, ‘Conophytum baccatum and its relatives: The introduction of a new Conophytum from Namaqualand, C. confusum’, Bradleya 33, 39–47.