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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.

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 km² 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;

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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



Source: Photographs taken by Andrew J. Young

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 (SKn1); (b) *Conophytum subterraneum* flowering in quartz gravel in the Kahams Mountain Desert vegetation unit (Dg5); (c) *Conophytum obcordellum* ssp. *obcordellum* 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 2700 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 marnerianum* and *Conophytum cupreiflorum*) are natural hybrids and are excluded on that basis. A further five (*Conophytum fibuliforme*, *Conophytum herreanthus* ssp. *herreanthus*, *Conophytum inornatum*, *Conophytum lithopsoides* 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 polyploid 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

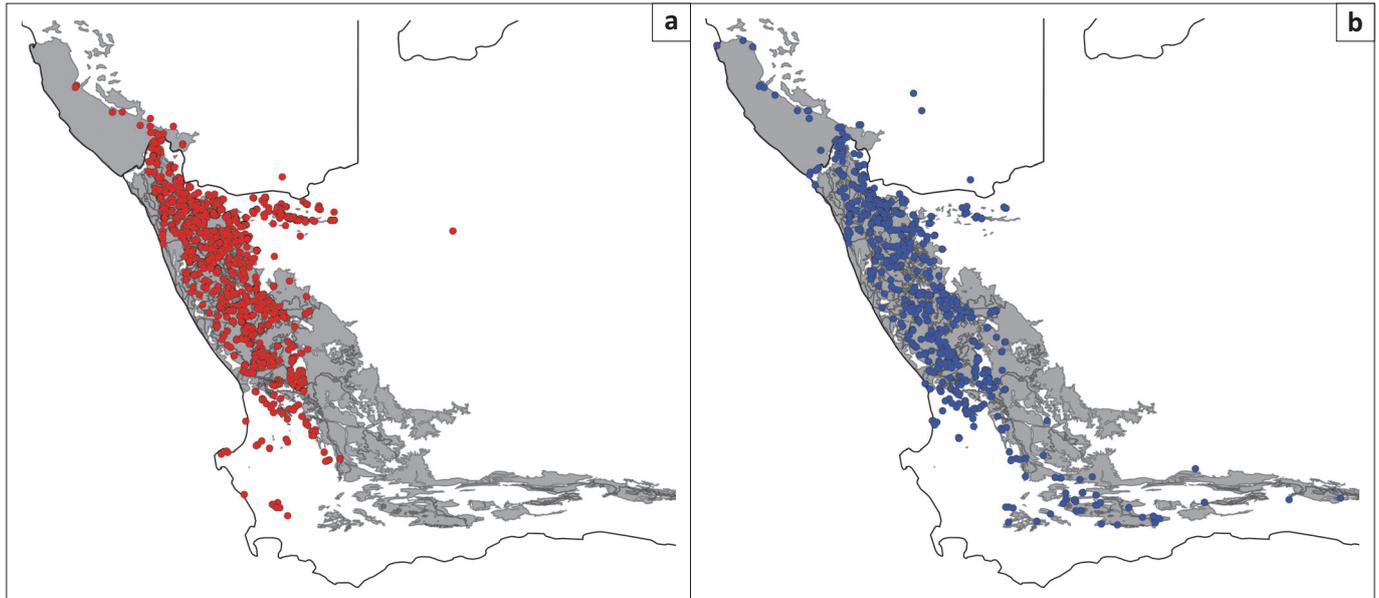
Vegetation Map of South Africa, Lesotho and Swaziland (Mucina & Rutherford 2006; South African National Biodiversity Institute [SANBI] 2009). For Namibia, the vegetation map of Giess (1971) was used. Shapefiles for conservation areas (formal, informal and focus areas) were also obtained from the SANBI. 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 2798 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 Sperrgebiet 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 taxa extend the range of the genus north to Luderitz in Namibia (*Conophytum saxetanum* and *Conophytum halenbergense*) and south and east to Steytlerville (*Conophytum truncatum*).

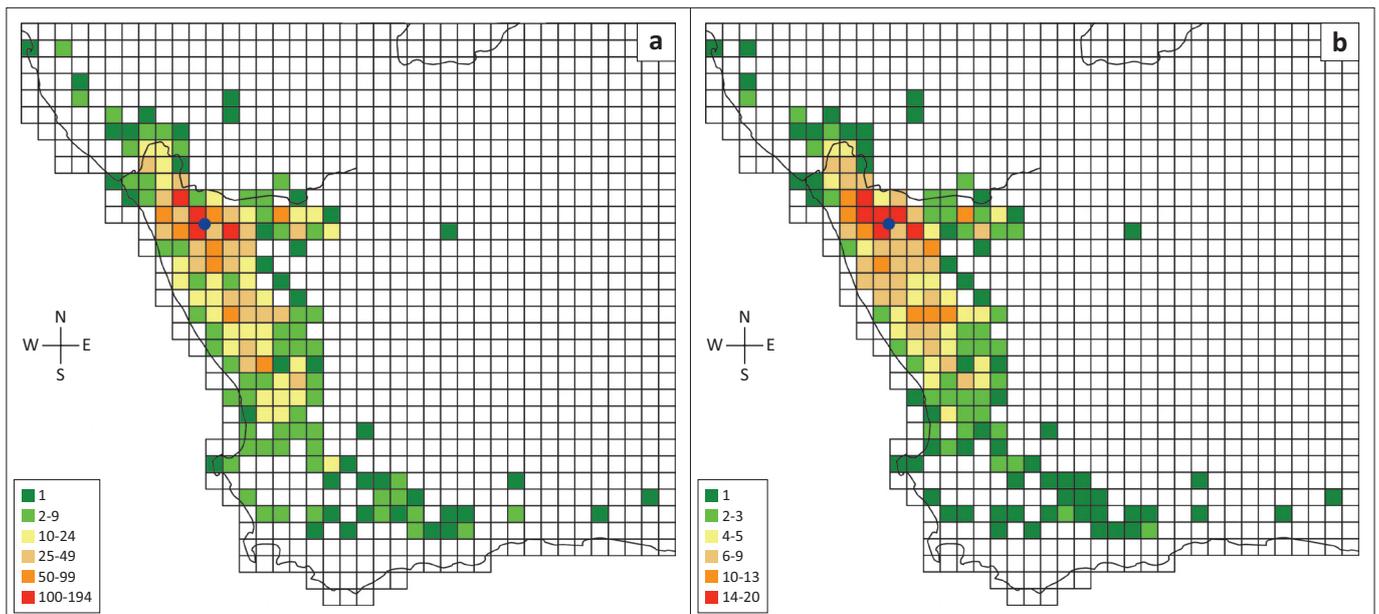
Mapping the distribution onto the recognised biomes of the region reveals a very strong association with the Succulent Karoo (Figures 2a and 2b). Almost 83% of all recorded *Conophytum* populations are located solely within this biome (Figure 4). The majority of the remaining observations are found within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



Source: Authors' own creation

Note: The Succulent Karoo biome is shaded.

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.



Source: Authors' own creation

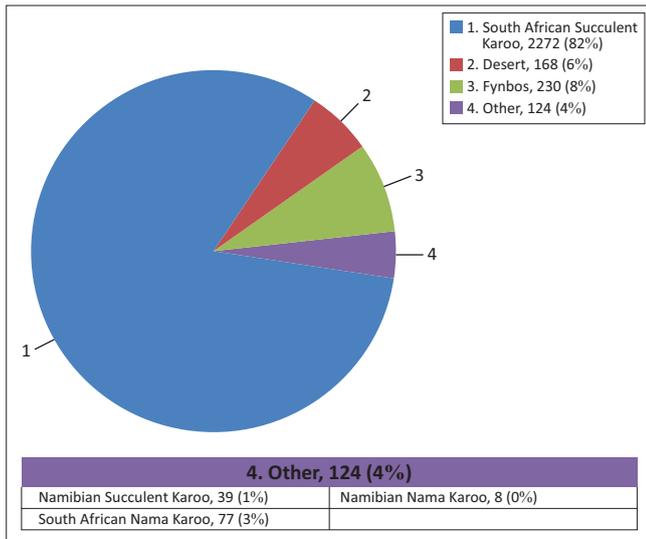
Note: The town of Steinkopf is marked by a blue circle.

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).

recorded populations in the Nama Karoo biome as it is currently geographically defined.

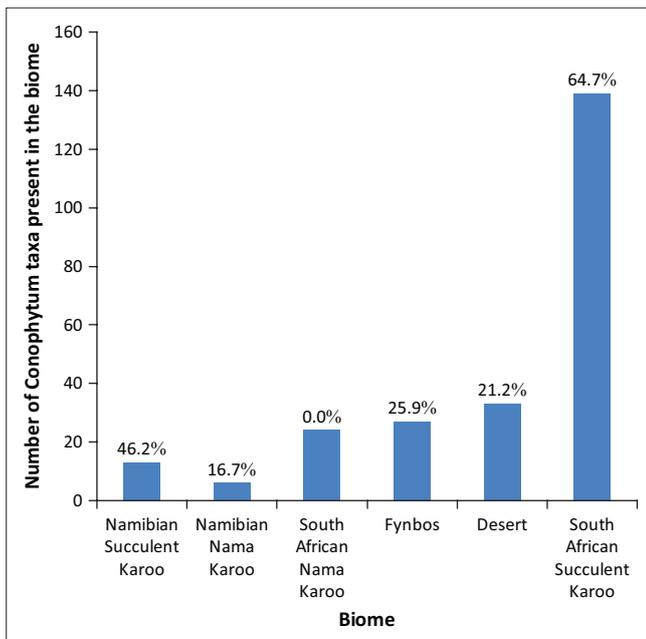
The occurrence of individual taxa (to subspecies level) across all the region's biomes is shown in Figure 5. Here the close association of the genus with the Succulent Karoo (predominantly in South Africa rather than Namibia) is once again evident with 94% of all recognised *Conophytum* taxa recorded 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 loeschianum* 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.



Source: Authors' own creation

FIGURE 4: Number of populations of *Conophytum* taxa (species and subspecies) recorded in the biomes of South Africa and Namibia in the Conobase.



Source: Authors' own creation

FIGURE 5: Number of recorded *Conophytum* taxa (species and subspecies) and the percentage of those taxa endemic to the biomes of South Africa and Namibia.

Succulent Karoo Biome

The Succulent Karoo alone is home to 149 *Conophytum* taxa, including 65 separate species. However, within this biome, the distribution of the genus across the recognised bioregions (Mucina & Rutherford 2006; Table 1) and their vegetation units (Table 2) varies greatly. The vast majority of taxa are found within the Namaqualand Hardeveld bioregion (84 taxa, with > 50% being endemic to the bioregion), especially the Namaqualand Klipkoppe Shrubland (SKn1) and Namaqualand Blomveld (SKn3) vegetation units (Table 3). Namaqualand Klipkoppe Shrubland is the single most important vegetation unit for the genus with 66 separate taxa, including 23 taxa endemic to that vegetation unit. Elsewhere 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-Escarpment 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 NKb3 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 <i>Conophytum</i> taxa represented in the bioregion (%)	Number of taxa endemic to the bioregion	Proportion of total <i>Conophytum</i> 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
Nama Karoo	Western Fynbos Renosterveld	4	2.5	0	0.0
	Bushmanland	22	13.8	0	0.0
Succulent Karoo	Lower Karoo	1	0.6	0	0.0
	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
	Rainshadow 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 Richtersveld Sheet Wash Desert	1	0
		Dg5 Kahams Mountain Desert	10	2
		Dg6 Hellsloof Canyon Desert	3	0
		Dg7 Northern Nababiepsberge Mountain Desert	2	0
		Dg8 Southern Nababiepsberge 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 Lowland Desert	1	0
		Dn5 Western Gariep Hills Desert	7	0
		Bushmanland	NKb3 Bushmanland Arid Grassland	22
	NKb4 Bushmanland Sandy Grassland		2	0
	Lower Karoo	NK11 Gamka Karoo	1	0
	East Coast Renosterveld	FRs8 Breede Shale Renosterveld	1	0
	Eastern Fynbos Renosterveld	FFs28 Kouga Grassy Sandstone Fynbos	2	0
	Karoo Renosterveld	FRd2 Hantam Plateau Dolerite Renosterveld	1	0
		FRs1 Vanrhynsdorp Shale Renosterveld	3	0
		FRs2 Nieuwoudtville Shale Renosterveld	3	0
	Namaqualand Cape Shrublands	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
		FFd2 Leipoldtville Sand Fynbos	2	0
		FFs1 Bokkeveld 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	FFd4 Atlantis Sand Fynbos	1	0
		FFg2 Boland Granite Fynbos	1	0
	West Coast Renosterveld	FRg2 Swartland Granite Renosterveld	1	0
		FRs9 Swartland Shale Renosterveld	1	0
	West Strandveld	FS1 Lambert's Bay Strandveld	3	0
		FS2 Saldanha Granite Strandveld	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	
South Africa	Western Fynbos	Renosterveld			
		FFq3 Matjiesfontein Quartzite Fynbos	2	0	
		FFs23 North Swartberg Sandstone Fynbos	1	0	
		FFs32 Nardouw Sandstone Fynbos	3	0	
		FRs6 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 Kobbekop Succulent Shrubland		2	0	
	Namaqualand		Hardeveld		
		SKn1 Namaqualand Klipkoppe Shrubland	67	23	
		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 Goariiep Mountain Succulent Shrubland	4	1
	SKr4 Lekkersing Succulent Shrubland		12	1	
	SKr5 Vyftienmyl 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 Tatasberg Mountain Succulent Shrubland		1	0	
	SKr10 Die Plate Succulent Shrubland		5	0	
	SKr11 Rooiberg 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	
	Namaqualand Sandveld	SKs1 Richtersveld Coastal Duneveld	1	0	
		SKs7 Namaqualand Strandveld	13	0	
		SKs8 Namaqualand Coastal Duneveld	1	0	
		SKs10 Riethuis-Wallekraal Quartz Vygieveld	6	0	
		SKs11 Namaqualand Arid Grassland	4	0	
		Trans-Escarpment Succulent Karoo	SKt1 Western Bushmanland Klipveld	1	0
	SKt2 Hantam Karoo		5	0	
	Rainshadow Valley Karoo	SKv1 Doringrivier Quartzite Karoo	2	0	
		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 Savannah	DS-1 Karas Dwarf Shrubland	4
DST-2 Desert/Dwarf Shrub Transition				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	
	South Africa	Namibia
Desert Biome	<i>C. cubicum</i> †	-
	<i>C. ernstii</i> ssp. <i>ernstii</i>	-
	<i>C. jucundum</i> ssp. <i>jucundum</i>	-
	<i>C. marginatum</i> ssp. <i>littlewoodii</i>	-
	<i>C. subterraneum</i> †	-
Fynbos Biome	<i>C. comptonii</i>	-
	<i>C. minusculum</i> ssp. <i>minusculum</i>	-
	<i>C. minusculum</i> ssp. <i>aestiflorens</i> †	-
	<i>C. obcordellum</i> ssp. <i>rolfii</i>	-
	<i>C. swanepoelianum</i> ssp. <i>proliferans</i>	-
	<i>C. swanepoelianum</i> ssp. <i>swanepoelianum</i>	-
	<i>C. turrigerum</i>	-
Nama Karoo Biome	No endemics	<i>C. quaesitum</i> ssp. <i>densipunctum</i>
Succulent Karoo Biome	<i>C. achabense</i> †	<i>C. ernstii</i> ssp. <i>cerebellum</i>
	<i>C. acutum</i>	<i>C. halenbergense</i>
	<i>C. antonii</i> †	<i>C. klinghardtense</i> ssp. <i>klinghardtense</i>
	<i>C. arthurofago</i>	<i>C. klinghardtense</i> ssp. <i>baradii</i> †
	<i>C. auriflorum</i> ssp. <i>auriflorum</i>	<i>C. ricardianum</i>
	<i>C. auriflorum</i> ssp. <i>turbiniforme</i> †	<i>C. taylorianum</i> ssp. <i>taylorianum</i>
	<i>C. bachelorum</i> †	-
	<i>C. bicarinatum</i>	-
	<i>C. bilobum</i> ssp. <i>altum</i>	-
	<i>C. bilobum</i> ssp. <i>claviferens</i> †	-
	<i>C. bilobum</i> ssp. <i>gracilistylum</i>	-
	<i>C. bolusiae</i> ssp. <i>bolusiae</i>	-
	<i>C. bolusiae</i> ssp. <i>primavermum</i> †	-
	<i>C. brunneum</i> †	-
	<i>C. bruynsii</i> †	-
	<i>C. burgeri</i> †	-
	<i>C. buysianum</i> ssp. <i>buysianum</i>	-
	<i>C. buysianum</i> ssp. <i>politum</i>	-
	<i>C. calculus</i>	-
	<i>C. caroli</i>	-
	<i>C. carpianum</i>	-
	<i>C. chauviniae</i>	-
	<i>C. chrisocruxum</i> †	-
	<i>C. chrisolum</i> †	-
	<i>C. concavum</i>	-
	<i>C. concordans</i>	-
	<i>C. cylindratum</i>	-
	<i>C. ectypum</i> ssp. <i>brownii</i>	-
	<i>C. ectypum</i> ssp. <i>cruciatum</i> †	-
	<i>C. ectypum</i> ssp. <i>sulcatum</i> †	-
<i>C. francoiseae</i>	-	
<i>C. fraternum</i>	-	
<i>C. frutescens</i>	-	
<i>C. globosum</i>	-	
<i>C. hanae</i> †	-	
<i>C. hermarium</i>	-	
<i>C. herreanthus</i> ssp. <i>rex</i>	-	
<i>C. hyracis</i> †	-	
<i>C. irmae</i>	-	
<i>C. jarmilae</i> †	-	
<i>C. jouberti</i>	-	

Table 3 continues →

TABLE 3 (Continues...): *Conophytum* taxa (species and subspecies) endemic to Biomes in South Africa and Namibia.

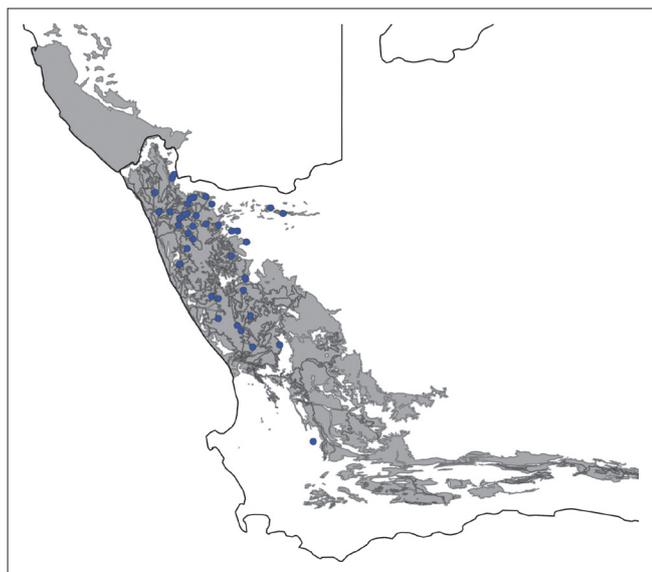
Biome	Species and subspecies	
	South Africa	Namibia
	<i>C. jucundum</i> ssp. <i>fragile</i>	-
	<i>C. jucundum</i> ssp. <i>jucundum</i>	-
	<i>C. jucundum</i> ssp. <i>marlothii</i>	-
	<i>C. jucundum</i> ssp. <i>ruschii</i>	-
	<i>C. lithopsoides</i> ssp. <i>koubergense</i> †	-
	<i>C. longibracteatum</i> †	-
	<i>C. maughanii</i> ssp. <i>armeniaceum</i>	-
	<i>C. maughanii</i> ssp. <i>latum</i>	-
	<i>C. meyeri</i>	-
	<i>C. minusculum</i> ssp. <i>leipoldtii</i>	-
	<i>C. mirabile</i> †	-
	<i>C. obcordellum</i> ssp. <i>stenandrum</i>	-
	<i>C. obscurum</i> ssp. <i>barbatum</i> †	-
	<i>C. obscurum</i> ssp. <i>sponsaliorum</i>	-
	<i>C. obscurum</i> ssp. <i>vitreopapillum</i> †	-
	<i>C. pellucidum</i> ssp. <i>cupreatum</i>	-
	<i>C. pellucidum</i> ssp. <i>saueri</i> †	-
	<i>C. phoeniceum</i>	-
	<i>C. piluliforme</i> ssp. <i>piluliforme</i>	-
	<i>C. piluliforme</i> ssp. <i>edwardii</i>	-
	<i>C. pium</i> †	-
	<i>C. quaesitum</i> ssp. <i>quaesitum</i>	-
	<i>C. regale</i> †	-
	<i>C. roodiae</i> ssp. <i>roodiae</i>	-
	<i>C. roodiae</i> ssp. <i>corrugatum</i>	-
	<i>C. roodiae</i> ssp. <i>sanguineum</i> †	-
	<i>C. schlechteri</i> †	-
	<i>C. smorenskaduense</i> †	-
	<i>C. stephanii</i> ssp. <i>stephanii</i> †	-
	<i>C. subfenestratum</i>	-
	<i>C. tantillum</i> ssp. <i>amicorum</i> †	-
	<i>C. tantillum</i> ssp. <i>heleniae</i> †	-
	<i>C. tantillum</i> ssp. <i>inexpectatum</i> †	-
	<i>C. tantillum</i> ssp. <i>lindenianum</i>	-
	<i>C. tantillum</i> ssp. <i>tantillum</i>	-
<i>C. taylorianum</i> ssp. <i>rosynense</i>	-	
<i>C. uviforme</i> ssp. <i>decoratum</i>	-	
<i>C. uviforme</i> ssp. <i>rauhii</i>	-	
<i>C. uviforme</i> ssp. <i>subincanum</i> †	-	
<i>C. vanheerdei</i> †	-	
<i>C. velutinum</i> ssp. <i>velutinum</i>	-	
<i>C. velutinum</i> ssp. <i>polyandrum</i>	-	
<i>C. verrucosum</i>	-	
<i>C. violaciflorum</i>	-	
<i>C. wettsteinii</i>	-	
<i>C. youngii</i> †	-	

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.

C., *Conophytum*.

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).



Source: Authors' own creation

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.

FIGURE 6: Distribution of the 45 *Conophytum* taxa (species and subspecies) regarded as point endemics.

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 (see Born *et al.* 2007). The level of endemism within each centre of the Greater Cape Floristic Region that possesses *Conophytum* is very high (33% – 59%), reflective of a high degree of habitat specialism.

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
<i>C. angelicae</i> ssp. <i>tetragonum</i>	<i>C. albiflorum</i>
<i>C. bilobum</i> ssp. <i>bilobum</i>	<i>C. comptonii</i>
<i>C. bolusiae</i> ssp. <i>bolusiae</i> †	<i>C. minusculum</i> ssp. <i>aestiflorens</i> †
<i>C. breve</i>	<i>C. minusculum</i> ssp. <i>minusculum</i>
<i>C. calculus</i> ssp. <i>calculus</i>	<i>C. obcordellum</i> ssp. <i>obcordellum</i> (var. <i>ceresianum</i>)
<i>C. calculus</i> ssp. <i>vanzylii</i>	<i>C. piluliforme</i> ssp. <i>edwardii</i>
<i>C. carpianum</i>	-
<i>C. cubicum</i> †	-
<i>C. depressum</i> ssp. <i>depressum</i>	-
<i>C. ernstii</i> ssp. <i>ernstii</i>	-
<i>C. francoiseae</i> †	-
<i>C. fraternum</i>	-
<i>C. hians</i>	-
<i>C. jouberti</i>	-
<i>C. jucundum</i> ssp. <i>fragile</i>	-
<i>C. jucundum</i> ssp. <i>marlothii</i>	-
<i>C. jucundum</i> ssp. <i>ruschii</i>	-
<i>C. loeschianum</i>	-
<i>C. luckhoffii</i>	-
<i>C. meyeri</i>	-
<i>C. minimum</i>	-
<i>C. minusculum</i> ssp. <i>minusculum</i>	-
<i>C. minutum</i>	-
<i>C. obcordellum</i> ssp. <i>obcordellum</i>	-
<i>C. obscurum</i> ssp. <i>obscurum</i>	-
<i>C. obscurum</i> ssp. <i>barbatum</i> †	-
<i>C. obscurum</i> ssp. <i>vitreopapillum</i> †	-
<i>C. pageae</i>	-
<i>C. pellucidum</i> ssp. <i>pellucidum</i>	-
<i>C. piluliforme</i> ssp. <i>piluliforme</i>	-
<i>C. quaesitum</i> ssp. <i>rostratum</i>	-
<i>C. roodiae</i> ssp. <i>roodiae</i>	-
<i>C. roodiae</i> ssp. <i>corrugatum</i>	-
<i>C. stephanii</i> ssp. <i>stephanii</i> †	-
<i>C. stephanii</i> ssp. <i>helmutii</i>	-
<i>C. stevens-jonesianum</i>	-
<i>C. subfenestratum</i>	-
<i>C. subterraneum</i> †	-
<i>C. taylorianum</i> ssp. <i>rosynense</i>	-
<i>C. truncatum</i> ssp. <i>truncatum</i>	-
<i>C. turrigerum</i>	-
<i>C. uviforme</i> ssp. <i>uviforme</i>	-
<i>C. uviforme</i> ssp. <i>decoratum</i>	-
<i>C. uviforme</i> ssp. <i>subincanum</i> †	-
<i>C. wettsteinii</i>	-

C., *Conophytum*.

†, point endemics.

TABLE 5: Distribution of *Conophytum* taxa (species and subspecies) within the major centres of the Greater Cape Floristic Region.

GCFR centre	Number of taxa	Number of endemics	Endemicity (%)
Cape Floristic Region	22	10	45
Hantam-Tanqua-Roggeveld region	3	0	0
Namaqualand region	80	42	53
Namib Desert region	27	9	33
Richtersveld centre	48	19	40
Other transition zone	32	19	59

Note: The genus is absent from the Karoo centre (see Born, J., Linder, H.P. & Desmet, P., 2007, 'The Greater Cape Floristic Region', *Journal of Biogeography* 34, 147–162).

GCFR, Greater Cape Floristic Region.

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

Vyftienmyl se Berge Succulent Shrubland, SKr9 Tatasberg Mountain Succulent Shrubland and SKr19 Aggeneys Gravel Vygieveld. Whilst these units are all relatively small in extent, they provide niche habitats for some succulents.

The absence of day-flowering taxa from the south-eastern extent of the distribution of the genus is not fully understood but is probably related to the absence of suitable pollinating vectors in the flowering season. Nocturnal flowering taxa are most frequented by moths, whilst day-flowering taxa are predominantly visited by pollen wasps (Jürgens & Witt 2014). A characteristic of the genus is that, with the exception of a handful of taxa, flowering displays a temporal shift compared to the vast majority of the Aizoaceae in the region (autumn and winter for the vast majority of *Conophytum* taxa and spring for most other genera). Jürgens and Witt (2014) suggested that the frequency of nocturnal flowering (as seen in approximately 25% of the genus) is a result of this temporal separation from other related genera. There does not appear to be any particular influence or association governing the distribution of those *Conophytum* taxa that display 'out-of-season' flowering (i.e. in spring or summer; data not shown). However, it is interesting to note that in describing a newly discovered species of *Conophytum*, Young *et al.* (2015) observed three pairings of closely related 'in-season' and 'out-of-season' flowering species in which both species from each pairing grew in close vicinity to each other at separate, range-restricted, sites. Although pollination in the genus is non-specialist (Jürgens & Witt 2014), incidences of natural hybrids are relatively uncommon, even in areas of high species richness (e.g. in the vicinity of Steinkopf). The best example occurs just to the east of Springbok, where dense colonies of *Conophytum ectypum* ssp. *brownii* (magenta flower) regularly hybridise with the less (locally) abundant *C. bilobum* (yellow flower) in the form of *C. × marnerianum* (red and orange flower forms). It is not understood why such hybridisation is only rarely observed, although species may be vertically stratified on a hillside.

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 the Namaqualand 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 smaleorum* 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 biome 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 (Rebello *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 schlechteri* 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 in the Namib Desert. Within its range, several forms of *C. pageae* can be readily identified, including the grey-bodied *udabibense* form from Namibia, the large *subrisum* form found around Kliprand on the south-western edge of Bushmanland and the tiny red-lipped form from the Garies area.

Examples of point endemism in *Conophytum* are common, especially within the Succulent Karoo, and account for ~28% of all taxa (see Table 3 and Figure 6). The Namaqualand Klipkoppe Shrubland (SKn1) is the most species rich (66 taxa) and has most endemics (23) and most point endemics (14). Whilst point endemics have, by definition, an extremely restricted range, in *Conophytum* this may sometimes be measured in the hundreds or a few thousand square metres. Examples include *Conophytum tantillum* ssp. *amicorum*, *C. burgeri*, *C. jarmilae* and the more recently discovered *Conophytum youngii* – all of which are currently known to occupy areas < 2000 m². Such taxa are clearly highly vulnerable to both anthropogenic (especially mining and farming) and environmental threats. Whilst rare, a small number of point endemics (e.g. *C. achabense*) are found occupying a range-limited area that spans across parts of two contiguous vegetation units. The mapping of the genus in this study has revealed a clear centre for endemism lying to the west of the small town of Steinkopf in the southernmost part of the Richtersveld. This can be described as a florally diverse area characterised by the presence of multiple vegetation units (e.g. one particular QDS in the Succulent Karoo is host to nine vegetation units, all of which possess *Conophytum* taxa).

Data sets such as the Conobase can aid conservation planning, not only in terms of informing the National and Global Red Lists but also to help identify suitable areas for possible protection by informing the extent of endemism and species richness (when used alongside data for other genera and the presence of threats). It is worthwhile to note that less than a third of *Conophytum* taxa (47) are presently protected within existing formal conservation areas (e.g. *C. burgeri* adjacent to Black Mountain's mining operations at Aggeneys; see Table 4). This study would suggest that the quartz-rich areas in 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. *primavernum*) 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.

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