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Hotbeds of diversity in the dwarf succulent genus *Conophytum* N.E.Br. (Aizoaceae, Ruschioideae, Rushieae): floral and genetic diversity in species-rich communities

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Abstract

Background A range of floral traits across four geographically separate species-rich communities of the dwarf succulent *Conophytum* N.E. Br. (Aizoaceae), a highly threatened genus in South Africa, have been examined.

Results In each community, individual species can be both partitioned and grouped on the basis of phylogenetic relatedness, floral characteristics, anthesis and phenology. Differences in the seasonality of flowering are relatively uncommon, while differences in anthesis are prevalent across the genus and a feature of each community. Within both nocturnal and diurnal flowering species, variation in floral structure, colour or pollen structure serve to separate the majority of species.

Conclusions Together, this suggests that separation of pollination systems is a key factor in maintaining community structure and species diversity. Given the high threat status of many species in the genus, species-rich patches could present an opportunity for future conservation strategies, where these complex communities rather than individual species are prioritised for conservation to preserve genetic and species diversity.

Keywords Biodiversity, Flower, Greater Cape Floristic Region, Habitat, Pollination, Quartz, South Africa

Background

The dwarf succulent genus *Conophytum* N.E.Br. is one of the most speciose in the Aizoaceae with 106 species, a significant proportion (~20%) of which are point endemics, often restricted to an area of < 1,000 m^2 [1, 2]. Such highly range-restricted species are a common feature within the arid parts of the Greater Cape Floristic Region (GCFR), notably in the Aizoaceae that are predominant in the Succulent Karoo Biome or Extra Cape Region [3–6]. *Conophytum* species occupy very small microhabitats due to their diminutive size, consisting of a single highly reduced pair of leaves (with some exceptions [7]). This enables them to divide the landscape into very small units [2, 8], exploiting many habitats in a small area,

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often resulting in the formation of complex species communities where up to 11 *Conophytum* species may occur sympatrically [3, 9]. It is not clear how so many species of the same genus that co-exist in close proximity, are able to maintain their genetic integrity [3, 10]. Complex species communities within the GCFR have also been reported in other genera, for example *Gladiolus* L. [11–12], although on a far less localised scale. A study of pollination shifts in *Gladiolus* found that species that occur together display shifts in phenology (flowering season), in response to pollination competition [12].

The majority of *Conophytum* species flower in autumn, while the peak flowering season in the family is from winter to spring [13]. A few species of *Conophytum*, however, display a shift in phenology, and flower in other seasons [14]. This has been observed in species that are found together in complex *Conophytum* communities throughout the distribution of the genus [2–3]. More commonly, *Conophytum* species display a range of anthesis (flower opening time) across the genus [7, 14]: diurnal (10.00–17.00); nocturnal (after dusk to just before dawn); afternoon (12 0.00–16.00); late afternoon (just before dusk to a few hours thereafter) [3, 7, 14]. Such a temporal range is rare in the Aizoaceae, but has been reported also in *Mesembryanthemum* subgenus *Phyllobolus* (N.E.Br.) Klak section *Vesperifolia* Haw [15, 16].

While the majority of Aizoaceae possess unspecialised radiate flowers [17], *Conophytum* has uniquely tubular flowers [18] with a range of floral structures [10, 14]. *Conophytum* species also exhibit a wide range of floral scents [19], flower colour as well as variability in the morphology of pollen [20], and the presence or absence of filamentous staminodes [7]. The flowers of *Erepsia* N.E.Br. also include a number of different floral structures, namely, the shape of the hypanthium, arrangement of staminodes, and the accessibility of nectar and pollen to pollinators. and a wide range of pollinators have been recorded visiting them, suggesting the various structures are strongly linked to different pollinators [21]. Few observational studies on pollination have been conducted on *Conophytum* [3, 22], with pollen wasps (Vespidae) and moths (Lepidoptera), as well as some members of Coleoptera, Diptera and Hymenoptera, recorded as the most common visitors of diurnal and nocturnal *Conophytum* flowers. Moths were found to be the main visitors and pollinators of the nocturnal flowering *Conophytum* species [3, 22]. Although there is some indication of specialisation in diurnal flowers to pollination by pollen wasps [22], this specialisation does not explain the great diversity of floral morphology in the genus, specifically among the diurnal species.

Floral diversification is commonly thought to be driven by pollination [12, 23–24] and thus the variation of floral traits in *Conophytum* may be a response to competition for pollinators or to reduce heterospecific pollen transfer between species within a community. Phylogenetic analyses of *Conophytum* indicate that differences in phenology and anthesis, as well as floral structure, have evolved several times across the genus and present strong phylogenetic signal in some instances, e.g. shifts from autumn to winter flowering, diurnal to nocturnal anthesis and shifts to a more radiate floral structure [14]. There are several shifts in floral syndromes in the genus, some that have evolved independently multiple times across clades, suggesting that these shifts may be driven by adaptations to pollination [14]. However, the nature of these floral traits, as well as the variation of other traits associated with flowering within complex *Conophytum* communities is unknown. There is also evidence of genetic connectivity between populations over large distances, specifically in the Bushmanland Inselberg Region (BIR) of South Africa. This may be due to pollinators traveling great distances between populations, and long-distance dispersal via anemochory due to the light and papery capsules of *Conophytum* species [25].

In this study, floral and genetic diversity within four species-rich *Conophytum* communities were assessed to investigate possible drivers of diversification in the genus. *Conophytum* is now one of the most threatened groups of plants in South Africa, with 96% of its species assigned a threat status of Vulnerable or higher (SANBI Red List, https://redlist.sanbi.org/; [26]). Understanding the com position and diversity of these species-rich communities could provide an alternative strategy to conservation, where the protection of species-rich communities of succulents is prioritised, rather than individual species.

Materials and methods

All datasets analysed in the present study are available upon request from the authors.

Selection of species-rich *Conophytum* communities

The species diversity of *Conophytum* was mapped using comprehensive distribution records [9] and four areas of high species diversity (10–20 co-occurring taxa), consisting of defined communities, e.g., a mountain or series of inselbergs, were identified for community analyses. The four communities selected lie within a longitude of -29.0 ° -29.6° and a latitude of 17.1° – 19.2°. The four span the winter-summer rainfall gradient as well as a temperature gradient [27] in Namaqualand in the northern parts of the GCFR. These sites are amongst the most speciose communities of *Conophytum* [9].

Community One is a mountainous area of approx. 22 km^2 located just inland of the north-western coast of South Africa. It receives winter-rainfall and intercepts coastal fog that develops in the west and moves eastwards [28–30] throughout the year. It comprises a range

of habitats and geologies, including quartz and gneiss, and these mountains host a range of unusual species, including monotypic genera of the Aizoaceae [13], and nine species of *Conophytum* (Table 1).

Community Two encompasses an area of approximately 70 km^2 that is characterised by large quartz patches. The area receives winter rainfall and intercepts some of the coastal fog [28–30] that moves inland. This community occurs in the highest area of diversity for the genus [9] with 11 species (including two subspecies of *C. flavum* N.E.Br.) recorded (Table 1).

Community Three comprises a chain of small inselbergs on the western edge of the BIR with a total area of approximately 28.5 km^2. The community straddles the winter-summer rainfall boundary, with the possibility of receiving both winter and summer rainfall, although in some years it may not receive any. Quartz is the dominant geology in the area, with *Conophytum* species found on quartz outcrops and quartz flats on the top and at the base of the inselbergs. *Conophytum* species are confined to these inselbergs as the surrounding lowland habitat adjacent to the inselbergs is dominated by Nama Karoo grasses and sands. A total of nine *Conophytum* species are recorded in the community including some point-endemics (Table 1).

Community Four is the most easterly of the selected communities in an area that primarily receives summer rainfall. It includes the largest inselberg in the BIR, as well as the surrounding large inselbergs with a total area of 70 km^2. These are comprised of metamorphosed granite (gneiss) with extrusions of quartz, which form quartz outcrops or quartz patches, providing suitable habitat for *Conophytum.* The high altitude and large size of these inselbergs means that they intercept moisture from winter-rainfall clouds moving across the landscape from the south-west, providing moisture during the winter period to those species occurring on the top and surrounding base of these inselbergs [31]. Although this community spans a large area, *Conophytum* species are restricted to the inselbergs, as the surrounding Nama Karoo vegetation does not provide suitable habitat for the genus. The community includes 11 *Conophytum* species, as well as some point endemics (Table 1).

Floral and genetic diversity analyses

Floral trait data (anthesis, phenology, flower structure, flower colour, presence / absence of filamentous staminodes, presence / absence of scent and pollen type) were obtained from [7, 20, 32–33] for each of the 38 species and subspecies of *Conophytum* within the four studied communities (Table 2). Additionally, flower (petaloid staminode) colour was determined using the RHS Colour Chart [34; Young unpublished data]. Figure 1 illustrates some of the main floral traits seen in the genus *Conophytum*. A Principal Coordinate Analysis (PCoA) was performed for floral traits of species in each of the communities using the 'R' package *ape* [35], employing Gower's coefficient.

Pairwise genetic distances of the species within a community were calculated based on data from [14] and

Table 1 *Conophytum* species and subspecies found within each species-rich community

Community one	Community two	Community three	Community four
C. bilobum (Marloth) N.E.Br. subsp. *altum* (L.Bolus) S.A.Hammer	*C. armianum* S.A.Hammer	*C. calculus* (A.Berger) N.E.Br. subsp. *vanzylii* (Lavis) S.A.Hammer	*C. achabense* S.A.Hammer
C. bolusiae Schwantes subsp. *bolusiae*	*C. bilobum (*Marloth) N.E.Br. subsp. *Bilobum*	*C. ectypum* N.E.Br. subsp. *ignavum* S.A.Hammer	*C. angelicae* (Dinter & Schwantes) N.E.Br. subsp. *angelicae*
C. breve N.E.Br.	*C. devium* G.D.Rowley subsp. *devium*	*C. hermarium* (S.A.Hammer) S.A.Hammer	*C. burgeri* L.Bolus
C. francoiseae (S.A.Hammer) S.A.Hammer	*C. ectypum* N.E.Br. subsp. *ectypum*	*C. lithopsoides* L.Bolus subsp. *lithopsoides*	*C. calculus* subsp. *vanzylii*
C. hians N.E.Br.	*C. flavum* N.E.Br. subsp. *flavum*	*C. lydiae* (H.Jacobsen) G.D.Rowley	*C. fulleri* L.Bolus
C. jucundum (N.E.Br.) N.E.Br. subsp. *marlothii* (N.E.Br.) S.A. Hammer	*C. flavum* N.E.Br. subsp. *novicium* (N.E.Br.) S.A.Hammer	*C. marginatum* Lavis subsp. *marginatum*	*C. limpidum* S.A.Hammer
C. meyeri N.E.Br.	*C. herreanthus* S.A.Hammer subsp. *herreanthus*	*C. maughanii N.E.Br.* subsp. *maughanii*	*C. lydiae* (H.Jacobsen) G.D.Rowley
C. obscurum N.E.Br. subsp. *barbatum* (L.Bolus) S.A.Hammer	*C. longum* N.E.Br.	*C. smorenskaduense* de Boer	*C. marginatum* Lavis subsp. *karamoepense* (L.Bolus) S.A.Hammer
C. stephanii Schwantes subsp. *stephanii*	*C. maughanii* N.E.Br. subsp. *latum* (Tischer) S.A.Hammer	*C. vanheerdei* Tisch	*C. maughanii* N.E.Br. subsp. *maughanii*
	C. pageae N.E.Br.		*C. praesectum* N.E.Br.
	C. phoeniceum S.A.Hammer		*C. ratum* S.A.Hammer
	C. stephanii Schwantes subsp. *helmutii* (Lavis) S.A.Hammer		

Table 2 Species recorded in each of the selected communities and floral traits coded for the species within each community. Phenology (flowering season): AUT = autumn, WIN= winter, SPR = spring, SUM = summer; Anthesis (flowering time): A = afternoon, D = diurnal, N = nocturnal; Flower Structure is coded according to the floral structures defined by [10]; Filamentous Staminodes: A = absent, P = present; Floral Scent: A = absent, P = present; Flower Colour: O = orange, P = pink, Pu = purple, R = red, W = white, Y = yellow. Pollen Type (1–6) defined by [20]. The number in parenthesis refers to the coding given in Figs. 3, 4, 5 and 6

Species	Phenology	Anthesis	Flower structure	Filamentous staminodes	Floral scent	Flower colour	Pollen type
Community one							
C. bilobum subsp. *altum* (1)	AUT	D	A2	A	A	Y	3
C. bolusiae subsp. *bolusiae* (2)	SPR/SUM	D	B1	A	A	Pu	2
C. breve (3)	AUT	N	A2	A	P	Y/O	4
C. francoiseae (4)	SPR/SUM	D	A2	A	A	Pu	3
C. hians (5)	AUT	N	B1	A	P	W/P/O/R	4
C. jucundum subsp. *marlothii* (6)	AUT	D	A2	A	A	P/Pu	3
C. meyeri (7)	AUT	D	B1	A	A	Y	2
C. obscurum subsp. *barbatum* (8)	AUT	D	B1	A	A	P/Pu	3
C. stephanii subsp. *stephanii* (9)	AUT	N	A2	A	P	W/Y/P/R	4
Community two							
C. armianum (1)	AUT	N	B1	A	P	P/O	4
C. bilobum subsp. *bilobum* (2)	AUT	D	A2	A	A	Y	3
C. devium subsp. *devium* (3)	AUT	D	A2	P	P	P	2
C. ectypum subsp. *ectypum* (4)	AUT	D	B1/B2	P	A	W/Y/P/Pu	3
C. flavum subsp. *flavum* (5)	AUT	D	B1	A	A	Y	2
C. flavum subsp. *novicium* (6)	AUT	D	B1	A	A	Y	3
C. herreanthus subsp. *herreanthus* (7)	AUT	D	A1	P	P	W/P	2
C. longum (8)	AUT	D	B1	P	P	W/Pu	2
C. maughanii subsp. *latum* (9)	AUT	N	A2	P	P	W/Y/P	4
C. pageae (10)	AUT	N	A2	A	P	W/Y/P/O/R	4
C. phoeniceum (11)	AUT	N	B1	A	P	P/R	4
C. stephanii subsp. *helmutii* (12)	AUT	N	A2	A	P	O/R	4
Community three							
C. calculus subsp. *vanzylii* (1)	AUT	N	A2	A	P	W/Y/P	4
C. ectypum subsp. *ignavum* (2)	AUT	D	B1/B2	P	A	P	3
C. hermarium (3)	AUT	D	A2	A	A	Pu	5
C. lithopsoides subsp. *lithopsoides* (4)	AUT	D	B2	P	A	W/P/Pu	3
C. lydiae (5)	AUT	D	A1	P	P	W/P	2
C. marginatum subsp. *marginatum* (6)	AUT	D	B1	P	P	P/Pu	1
C. maughanii subsp. *maughanii* (7)	AUT	N	A2	P	P	W/Y/P	4
C. smorenskaduense (8)	WIN	D	A2	P	A	W/Y/Pu	1
C. vanheerdei (9)	AUT	D	B1	A	A	Pu	3
Community four							
C. achabense (1)	AUT	A	B1	A	P	Pu	2
C. angelicae subsp. *angelicae* (2)	AUT	N	A2	A	P	R	4
C. burgeri (3)	AUT	A	A2	P	P	W/P	1
C. calculus subsp. *vanzylii* (4)	AUT	N	A2	A	P	W/Y/P	4
C. fulleri (5)	AUT	D	A2	A	P	W/P/Pu	2
C. limpidum (6)	AUT	D	A1	P	P	W/P	2
C. lydiae (7)	AUT	D	A1	P	P	W/P/Pu	1
C. marginatum subsp. *karamoepense* (8)	AUT	D	B1	P	P	P/Pu	6
C. maughanii subsp. *maughanii* (9)	AUT	N	A2	P	P	W/P/Y	4
C. praesectum (10)	AUT	D	A1	A	P	P/Pu	2
C. ratum (11)	AUT	A	A1	A	P	P/Y	2



Fig. 1 Examples of *Conophytum* species displaying a range of flowering traits: (**A**) *C. bilobum* subsp. *altum* (diurnal flowering, autumn); (**B**) *C. burgeri* (afternoon, autumn) with insect pollinator; (**C**) *C. pageae* (nocturnal, autumn); (**D**) *C. smorenskaduense* (diurnal, winter); (**E**) *C. hians* (nocturnal, autumn)

presented in a PCoA. The maximum likelihood (ML) tree for *Conophytum* [14] was used to calculate pairwise genetic values for each species using the *cophenetic.phylo* function in the 'R' package 'ape' [35–36]. This was performed at species level as molecular data on individual subspecies was not available. The pairwise distances for each of the species in the community were manually compiled into separate matrices and a PCoA was performed using the 'R' tool *pcoa*, available from the package 'ape' [35] for each of the four communities. The PCoAs were plotted using the *biplot* function [35] and the axes were set to a standard scale across the communities.

Environmental variables

Downscaled 1 km^2 resolution climate layers were sourced from the AFRICLIM database [37] representing mean climate between 1950 and 2000. Layer preparation and downscaling followed the procedure in [37]. In addition to climatic variables, a high-resolution digital elevation model (DEM, 30 m^2) for the study region, and lower resolution geology layer categorising the region into six geological categories (1 km^2), were acquired from P. G. Desmet. Slope and aspect layers were calculated from the DEM using the function terrain in the package *raster* [38] in R (R core team, 2020). To reduce the number of climate variables, Pearson's correlation co-efficient was used. Correlation coefficients were calculated on all pairs of climate variables for all species occurrence points used for the climatic variables. Six climate variables were kept after removing all highly correlated variables (Pearson's coefficient greater than 0.8 or less than – 0.8): Bio 1 (mean annual temperature), Bio 2 (mean diurnal range), Bio 3 (Isothermality), Bio 11 (Mean temperature of the coldest quarter), Bio 13 precipitation in the wettest month), Bio 14 (precipitation in the driest month). In addition, elevation and slope were included in the analysis [39].

Results

Environmental niche

The *Conophytum* species that comprise each of the four communities possess varied environmental niche breadths and form distinct clusters even though some species are found in more than one community (e.g., *C. bilobum* (Marloth) N.E.Br.) (Fig. 2). By contrast to the others, the environmental breadth of Community Three is very tightly clustered. Although each community comprises both narrow- (e.g., *C. smorenskaduense* de Boer) and wide-range endemics (i.e., extending well beyond the community, e.g., *C. pageae* N.E.Br.), the geographical extent of those present in Community Three is much smaller. Community Three lies on the transition boundary between winter- and summer-rainfall areas, whereas

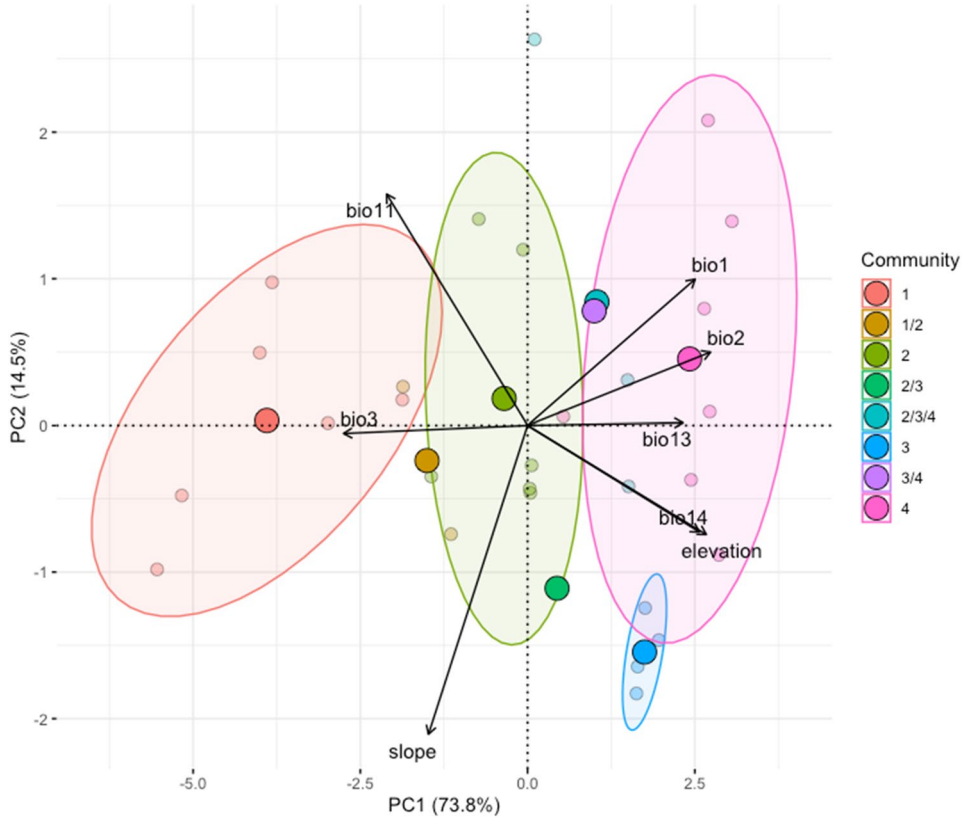

Fig. 2 Principal component analysis of *Conophytum* species based on eight continuous environmental variables (Bio 1 (mean annual temperature), Bio 2 (mean diurnal range), Bio 3 (isothermality), Bio 11 (mean temperature of the coldest quarter), Bio 13 (precipitation in the wettest month), Bio 14 (precipitation in the driest month), slope and elevation. Species belonging to the four communities are colour coded. Note that some species are found in more than one community

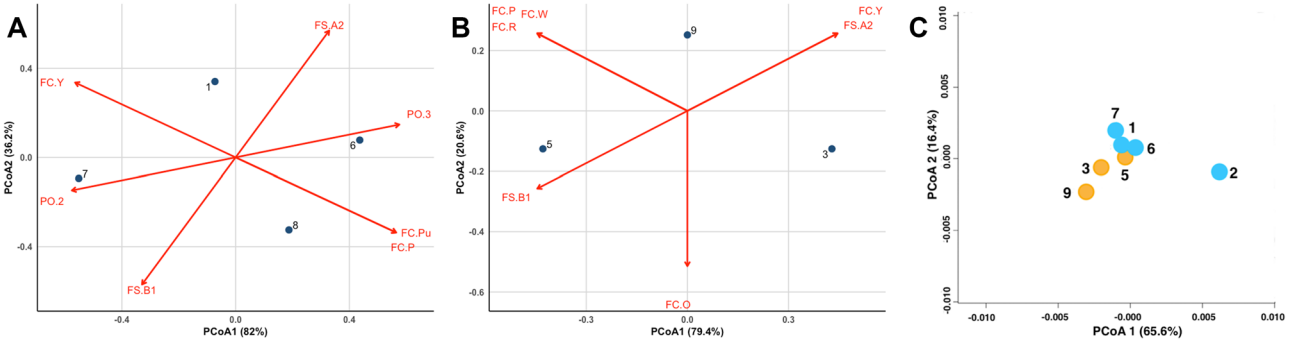

Fig. 3 Principal coordinate analysis of *Conophytum* species in community one: (**A**) flower structure (FS), flower colour (FC) and pollen type (PO) of autumnal flowering diurnal species; (**B**) flower structure and flower colour of nocturnal species; and (**C**) pairwise genetic distance (blue = diurnal flowering, orange = nocturnal flowering). 1 – *C. bilobum* subsp. *altum*, 2 – *C. bolusiae* subsp. *bolusiae*, 3 – *C. breve*, 4 – *C. francoiseae*, 5 - *C. hians*, 6 – *C. jucundum* subsp. *marlothii*, 7 – *C. meyeri*, 8 – *C. obscurum* subsp. *barbatum*, 9 - *C. stephanii* subsp. *stephanii*

Communities One and Two experience winter rain and Community Four late summer / early autumn rain.

Community one

The floral traits, anthesis and phenology separate the species in Community One into three groups (Table 2; Fig. 3A): a group of four diurnal autumnal flowering species, a nocturnal autumnal flowering group with three species and a diurnal spring-to-summer flowering group with two species. Both *C. bolusiae* subsp. *bolusiae* Schwantes and *C. francoiseae* (S.A.Hammer) S.A.Hammer are temporally separated from the other species by differences in phenology, flowering in spring to summer rather than autumn but are distinguished from each other by floral structure (Table 2). The diurnal species that flower in autumn display differences in flower

structure, pollen type and flower colour (Fig. 3A). The proportion of variance is primarily explained by axis 1 (82%) and axis 2 (36,2%). The nocturnal species are separated by both flower structure (B1 in *C. hians* N.E.Br. and A2 in *C. breve* N.E.Br. and *C. stephanii* Schwantes subsp. *stephanii*), and colour (*C. breve* only displays light or dark yellow flowers; Table 2; Fig. 3B). The proportion of variance is explained by axis 1 (79.4%) and axis 2 (20.6%).

The PCoA of pairwise genetic distance for species included in the community (Fig. 3C) places the majority of species in a loose cluster, while *C. stephanii* (nocturnal) and *C. bolusiae* (diurnal) are the most distant. The proportion of variance is explained mainly by axis 1 (65.6%) and axis 2 (16.4%), while axes 3–7 only explained < 1%. Pairwise genetic distance of the species ranged from 0.001 to 0.009, with an average of 0.005. The diurnal species are genetically separated but it is worth noting that *C. bilobum* and *C. meyeri* N.E.Br. are positioned close to one another. The three nocturnal species are genetically distinct, placed almost equidistant from one another.

Community two

All species in Community Two flower in autumn, but differences in anthesis split them into two distinct groups representing the seven diurnal and five nocturnal species (Table 2). Floral traits serve to both group and separate the diurnal flowering species (Fig. 4A). *Conophytum bilobum* subsp. *bilobum* and both subspecies of *C. flavum* N.E.Br. are separated from the other species by the absence of filamentous staminodes and lack of scent. The subspecies of *C. flavum* are separated as they possess different pollen types. Flower colour also distinguishes species with a majority, but not all, possessing yellow flowers. *Conophytum ectypum* N.E.Br. subsp. *ectypum* is distinguished by its flower structure. The proportion of variance in this group of species is explained mainly by PCoA1 (62%) and PCoA2 (34.7%). The nocturnal flowering species *C. armianum* S.A.Hammer and *C. phoeniceum* S.A.Hammer share a B1 floral structure but they are separated by flower colour. Similarly, while *C. maughanii* N.E.Br. subsp. *latum* (Tischer) S.A.Hammer, *C. pageae* N.E.Br. and *C. stephanii* subsp. *helmutii* (Lavis) S.A.Hammer all share a common floral structure, the first possesses white to purple filamentous staminodes and the last has a red-orange flower colour (Table 2; Fig. 4B). PCoA 1 captures 77.4% of the variation and PCoA 2 21.1%, together representing 98.5% of the difference between the species.

The PCoA of pairwise genetic distance shows that the majority of species are closely grouped together, with the exception of four species of which *C. longum* N.E.Br. is the most isolated (Fig. 4C). Of the diurnal flowering species in Community Two, *C. bilobum* and *C. ectypum* are close to one another, with the other species positioned separately from one another. *Conophytum stephanii* is the most genetically isolated species in the nocturnal species guild. Variance in the PCoA is explained by nine axes, with the largest proportion of variance explained by axis 1 and 2, with proportions of 45.4% and 32.0%, respectively. The average pairwise genetic distance of the species is 0.006 (within the range 0.002–0.012).

Community three

Three groups of species can be determined in this community based on anthesis and phenology (Table 2). The majority of species are autumnal, separated by differences in anthesis with *C. maughanii* subsp. *latum* and *C. calculus* (A.Berger) N.E.Br. subsp. *vanzylii* (Lavis) S.A.Hammer flowering at night. *Conophytum smorenskaduense* is separated from all other species in this community in both anthesis and phenology as it flowers both in the afternoon and in winter. The diurnal autumnal species are separated by their floral characters (Fig. 5A). Floral structure separates both *C. hermarium* (S.A.Hammer)

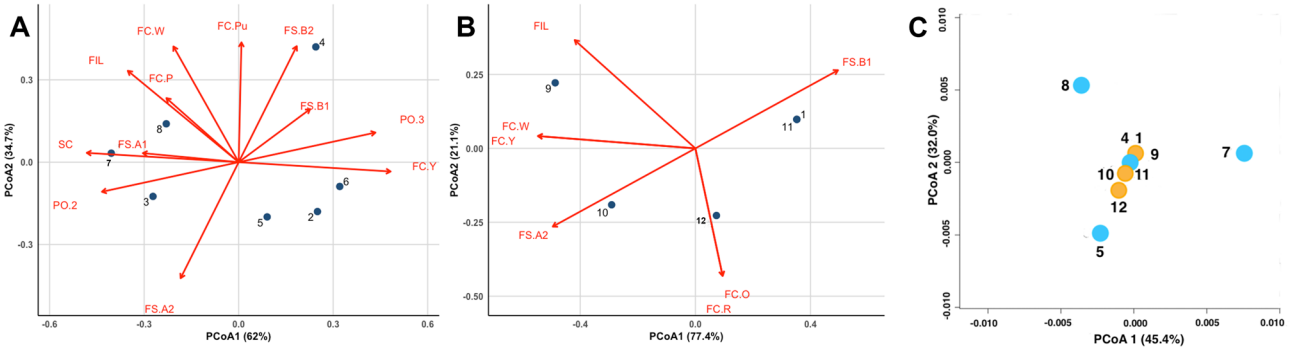

Fig. 4 Principal coordinate analysis of *Conophytum* species in community two: (**A**) flower structure (FS), flower colour (FC), presence of filamentous staminodes (FIL), presence of scent (SC) and pollen type (PO) of diurnal species; (**B**) flower structure, flower colour, presence of filamentous staminodes and presence of scent of nocturnal species; and (**C**) pairwise genetic distance (blue = diurnal flowering, orange = nocturnal flowering). 1 - *C. armianum*, 2 - *C. bilobum* subsp. bilobum, 3 - *C. devium subsp.* devium, 4 - *C. ectypum* subsp. *ectypum*, *5* - *C. flavum* subsp. *flavum*, 6 - *C. flavum* subsp. *novicium*, 7 - *C. herreanthus* subsp. *herreanthus*, 8 - *C. longum*, 9 - *C. maughanii* subsp. *latum*, 10 - *C. pageae*, 11 - *C. phoeniceum*, 12 - *C. stephanii* subsp. *helmutii*

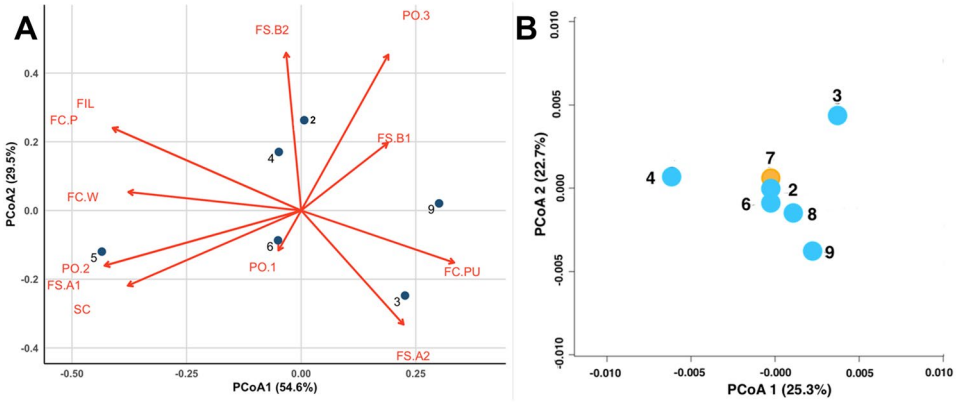

Fig. 5 Principal coordinate analysis of *Conophytum* species in community three: (**A**) flower structure (FS), flower colour (FC), presence of filamentous staminodes (FIL), presence of scent (SC) and pollen type (PO) of diurnal flowering species; and (**B**) pairwise genetic distance (blue = diurnal flowering, orange = nocturnal flowering). 1 - *C. calculus* subsp. *vanzylii*, 2 - *C. ectypum* subsp. *ignavum*, 3 - *C. hermarium*, 4 - *C. lithopsoides* subsp. *lithopsoides*, 5 - *C. lydiae*, 6 - *C. marginatum* subsp. *marginatum*, 7 - *C. maughanii* subsp. *maughanii*, 8 - *C. smorenskaduense*, 9 - *C. vanheerdei*

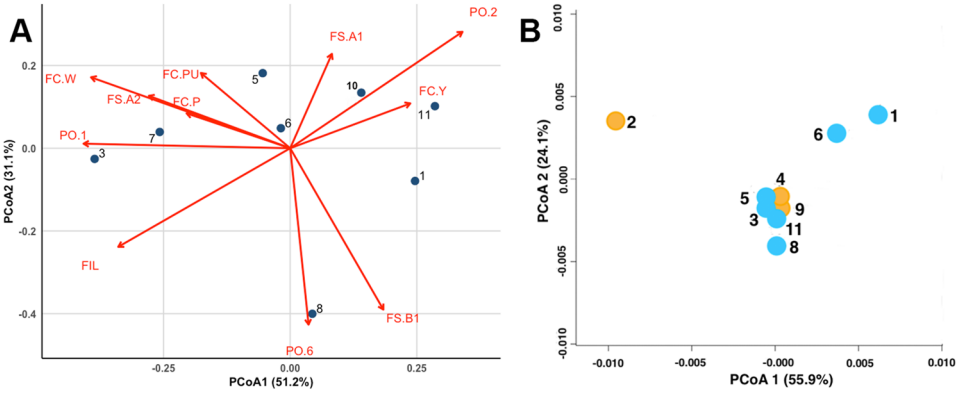

Fig. 6 Principal coordinate analysis of *Conophytum* species in community four: (**A**) anthesis (T), flower structure (FS), flower colour (FC) and pollen type (PO) of diurnal flowering species, (**B**) pairwise genetic distance (blue = diurnal flowering, orange = nocturnal flowering). 1 - *C. achabense*, 2 - *C. angelicae* subsp. *angelicae*, 3 - *C. burgeri*, 4 - *C. calculus* subsp. *vanzylii*, 5 - *C. fulleri*, 6 - *C. limpidum*, 7 -*C. lydiae*, 8 - *C. marginatum* subsp. *karamoepense*, 9 -. *maughanii* subsp. *maughanii*, 10 - *C. praesectum*, 11 - *C. ratum*

S.A.Hammer (A2) and *C. lydiae* (H.Jacobsen) G.D.Rowley (A1) from the other species. The presence of filamentous staminodes and a common flower structure (B2) group *C. ectypum* subsp. *ignavum* S.A.Hammer and *C. lithopsoides* L.Bolus subsp. *lithopsoides. Conophytum marginatum* Lavis subsp. *marginatum* also shares floral traits with *C. ectypum* subsp. *ignavum* and *C. vanheerdei* Tisch but is the only species in the guild to have scented flowers and pollen type 1 (also seen in *C. smorenskaduense*). The proportion of variance of the PCoA based on the floral traits in the diurnal autumnal species is largely explained by PCoA1 (54.6%) and PCoA2 (29.5%). The two nocturnal species possess scented flowers with a common A2 floral structure and flower colour but are separated by the presence of filamentous staminodes in *C. maughanii* subsp. *latum* (Table 2).

The PCoA of pairwise genetic distance in Community Three includes a loose grouping of species, namely *C. ectypum* and *C. maughanii* (placed very close together) together with *C. marginatum* and *C. smorenskaduense. Conophytum hermarium* and *C. lithopsoides* are most isolated (Fig. 5B). The proportion of variance is explained mainly by the first three axes (35.4%, 25.3% and 22.7%, respectively). The average pairwise genetic distance between the species is 0.006 (in the range 0.003–0.009).

Community four

The 11 species in Community Four are all autumn-flowering and only separated by anthesis (Table 2). The species form three distinct groups: afternoon-flowering species, a larger group of diurnal species and a small group of nocturnal species. Those species that flower throughout the day or in the afternoon are well-separated by floral traits (Fig. 6A). The A2 floral structure is seen in *C. lydiae*, but this is separated from *C. burgeri* L.Bolus and *C. fulleri* L.Bolus by its flower colour, which is never purple. Flower structure also groups *C. limpidum* S.A.Hammer, *C. praesectum* N.E.Br. and *C. ratum*

S.A.Hammer (A1) as well as *C. achabense* S.A.Hammer and *C. marginatum* (B1). However, *C. achabense* and *C. ratum* flower only in the afternoon, and not throughout the day as the other species. The species are further separated by flower colour and by the presence or absence of filamentous staminodes. The proportion of variance is largely explained by the PCoA 1 (51.2%) and PCoA2 (31.1%). Community Four includes three nocturnal taxa, *C. angelicae* (Dinter & Schwantes) N.E.Br. subsp. *angelicae*, *C. calculus* subsp. *vanzylii and C. maughanii* subsp. *maughanii* that share scented flowers and the same floral structure (Table 2). These are, however, separated by floral traits, such as the red-orange flowers in *C. angelicae* and the presence of filamentous staminodes in *C. maughanii*.

The pairwise genetic distance PCoA for this community presents a large grouping of species (*C. burgeri*, *C. calculus*, *C. fulleri*, *C. maughanii*, *C. ratum*), with four species separated from this group (Fig. 6B). *Conophytum marginatum* is positioned closest to this group, while *C. angelicae* is the most isolated and hence most distantly related species in this particular community. *Conophytum limpidum* and *C. achabense* are placed relatively close to one another, but do not form a group. The first and second axes of the PCoA explain the majority of the variance, with proportions of 55.9% and 24.1%, respectively. The average pairwise genetic distance for these species in the community is 0.007 and ranges from 0.003 to 0.016.

Discussion

Floral diversity in *Conophytum* communities

The distribution of *Conophytum* within southwestern Africa highlights two major features of the genus [9]. First, approx. a fifth of all species and subspecies are severely range-restricted and can be considered point-endemics. Second, right across the distribution of the genus, with the exception of the most northerly and eastern extents, several species are typically found together with diurnal and nocturnal flowering species often being sympatric. This includes the four communities examined here. A key feature is that the species in these four communities form temporal guilds, separated by both anthesis and phenology. As a result, species across the different temporal guilds would not compete for pollinators and would be reproductively isolated from one another, maintaining species integrity [40]. Phenological shifts between co-occurring species, as observed in *Conophytum* Communities One and Three (Table 2) have also been reported in *Gladiolus* [12]. *Gladiolus* forms complex species communities that co-occur within a Quarter Degree Square, however, they are not found sympatrically within a microhabitat [11, 12], as is the case in *Conophytum*. Nevertheless, *Gladiolus* exhibits similar flowering season shifts between closely occurring species, thought to be driven by pollination [12]. As the peak flowering season of *Conophytum* is in autumn, earlier than the majority of the Aizoaceae that dominate the GCFR, interspecific competition for pollinators can be considered high, with *Conophytum* providing one of the few floral resources in the region [22]. The known pollinators of *Conophytum* are thought to operate over relatively small spatial scales (including beetles, pollen wasps and moths; [3, 22]). The observed shifts in phenology in *Conophytum* are likely to be driven by pollination competition. Studies show that there is a strong pollinator specialisation and even co-divergence of plants and pollinators in the GCFR, with younger associations especially prevalent in the Succulent Karoo biome [41].

The shift in flowering season seen in Communities One and Three may be attributed to their location and associated climatic conditions. Community One includes the early (spring-to-summer) flowering *C. bolusiae* subsp. *bolusiae* and *C. francoiseae* and is positioned a few kilometres inland on the northwestern coast of South Africa. Although located in Namaqualand, with semi-desert climatic conditions, it intercepts coastal fog that develops just off the west coast and moves inland [30, 42]. This provides moisture and cooler temperatures during the summer and spring months, permitting these two taxa to flower in these otherwise hot and arid seasons. Community Three straddles the winter-summer rainfall boundary and the bimodal rainfall provides a longer climatic period suitable for flowering than in other communities. The increased possibility of summer rainfall has allowed the flowering season of *C. hermarium* to shift earlier into summer [7, 14]. A phenological shift is also seen in *C. smorenskaduense*, which is the only strictly winter flowering species in the genus [7, 14]. In addition, the shift in anthesis of *C. smorenskaduense* to the warmer winter afternoon hours may coincide with peak pollinator activity during this period. It is also worth noting that *C. smorenskaduense* and *C. hermarium* are morphologically near-identical and that several such morphologically-similar 'pairs' of *Conophytum* species are found in close proximity to each other elsewhere in South Africa, separated only by phenology (e.g., *C. bachelorum* S.A.Hammer and *C. confusum* A.J.Young, C.Rodgerson, S.A.Hammer and M.R.Opel, and *C. rugosum* S.A.Hammer and *C. youngii* C.Rodgerson; [2]).

The autumn flowering *Conophytum* species in the communities, which comprise the majority, are all separated by differences in anthesis. In Community Four, the diurnal species were separated further by anthesis, with *C. achabense* and *C. ratum* flowering only in the early afternoon, while flowers of *C. burgeri* only open in the late afternoon (Table 2). A similar range in anthesis was previously seen in the Aizoaceae in a section of

Mesembryanthemum (subgenus *Phyllobolus* section *Vesperifolia*) with both diurnal and nocturnal species as well as afternoon and late afternoon flowering species [15–16]. No conclusions were made suggesting why there are differences in anthesis, however, as the distribution of the species overlap; the switch is likely a means to avoid overload of heterospecific pollen. While minimising hybridisation and gene flow [40] may be a main driver, the differences in anthesis seen in sympatric *Conophytum* species may also be driven by competition for pollinators. Differences in anthesis are evident in all the communities studied, with a shift in anthesis between closely related species. Differences in phenology are rare in the genus, with the vast majority of species flowering in the autumn when pollinator abundance is much lower than spring [22]. Gene flow between species that occupy the same temporal niche (e.g., diurnal flowering species in a community) appears to be avoided or minimised by genetic dissimilarity.

Although there is a clear separation in flowering times between diurnal and nocturnal species, the distinction between diurnal and afternoon to late afternoon flowering species is not as well defined. Diurnal flowers are open from around 10.00 to 17.00, while afternoon flowers open around 12.00, closing a few hours later, i.e. flowers of both groups are open during the afternoon. In addition, the flowers of some species remain permanently open towards the end of the flowering season [3, 7]. It is not clear why there is such an overlap in anthesis between these species, as there are no clear barriers to prevent gene flow, however, this overlap may be attributed to competition and maximum allocation of pollination resources. Individuals of *Conophytum* within a population usually flower together resulting in a mass 'bouquet' effect presented by a number of contiguous flowers [3]. The mass flowering of such species in a community provides ample floral resources, and studies showed that pollinators forage on a mass of flowers at a time before moving onto another mass, rather than mixed foraging [43–44]. Due to the preference of mass foraging of pollinators, the shift in anthesis of *Conophytum* may be an adaptation towards pollination optimisation, with pollinators foraging on different floral masses of *Conophytum* throughout the day. This may be especially important in Community Four, as this is located at the very eastern edge of the winter-rainfall region, where pollinators may be limited.

Divergence of floral morphology

The groups of species that are separated by anthesis and phenology form temporal guilds within each community. Species within a temporal guild display a unique combination of floral traits, including flower structure, flower colour, pollen structure, absence or presence of floral scent and absence or presence of filamentous staminodes. As floral diversification is commonly thought to be driven by pollination [12], with the force of pollination diversification in plants driven by competition and adaptation to pollinators [12, 45–46], these drivers are believed to be one of the main factors driving floral divergence in *Conophytum.* The diverse floral morphology suggests an adaptation and specialisation to different pollinators, thus reducing the competition for pollination resources within the guild [12, 46]. Differences in pollen structure can be seen across the *Conophytum* species within a community. While this is most evident for nocturnal species (which all share a common pollen type not found in diurnal species) there are some differences between diurnal species that again might be linked to specific pollinator preferences [20]. The floral diversity of *Conophytum* is not only found within the sympatric communities, but also in the phylogenetic analyses of the genus, with floral traits likely to have evolved numerous times across the genus [14]. These traits include phenology, anthesis and floral structure, with inferred pollination shifts in *Conophytum* (based on anthesis and structure) having taken place every 1.8 species [14]. A similarly high rate of pollination syndromes shifts was found also in *Lapeirousia* Thunb. (Iridaceae) with 1.5 shifts per species [47]. There is considerable evidence that shifts in pollination syndromes lead to floral evolution [48–49], suggesting that the shifts observed in *Conophytum* and within the communities are driven and maintained by pollination.

The unique tubular flowers of *Conophytum* and range of floral structures suggests a specialisation towards pollinators [3]. Pollen wasps (*Quartina* spp.) were found to be frequent visitors, specifically of the diurnal flowering species, while moths were the main pollinators of the nocturnal species [3, 22]. As the pollen wasps have long proboscises, the unique tubular flowers of *Conophytum* may represent a specialisation towards these pollinators [3]. suggested that the inclusion of filamentous staminodes (which are variably absent or present in the flowers of *Conophytum*) encourages the pollinators to crawl down the tube. Although specialisation of *Conophytum* flowers towards pollen wasps is proposed, the position of the anthers and stigmas at the mouth of the tube does not restrict pollination from generalist pollinators in some cases, e.g. *C. subfenestratum* Schwantes visited most frequently by Malachiid beetles [3]. As *Conophytum* flowers represent a floral resource mostly unavailable in the region during autumn [22], they should be attractive to a range of pollinators, and may be pollinated by specialist as well as generalist pollinators. The relationship between the nocturnal *Conophytum* species and their pollinator is clearer, with the strongly scented tubular flowers inferring a strong adaptation to moth pollination [22], as well as possessing a unique pollen morphology [20]. Some of

the flowers of nocturnal *Conophytum* species are white, which is a common nocturnal moth-pollinated flower colour, while a few nocturnal species possess red/orange-coloured flowers (e.g., *C. stephanii* [7, 22]).

Flower colour across the genus is variable and some species display almost the full range of colours found in the Aizoaceae, including white, yellow, pink, red-orange and purple. Although flower colour is usually strongly driven by pollination specialisation [50–53], [3] found that different coloured *Conophytum* flowers present within a community were visited by insects. Flower colour in *Conophytum* also includes an inherent variation both across and, more rarely, within populations. For example, while *C. ratum* generally has pink flowers, there is a low incidence of yellow-flowering forms present in habitat. Such variation is most evident within some populations of nocturnal flowering species with several colour forms evident within a single group of plants in habitat (e.g., in *C. pageae*). Despite some overlap in flower colour, there is a degree of separation of flower colour between species in a community. Such distinction is likely to be related to pollination adaptation [52].

There is no information available on the UV reflective properties of different coloured *Conophytum* flowers (and hence the relative attractiveness to insects) but a study on *Erepsia* flowers (part of the Greater Cape flora) showed that flower colour was associated with pollination by beetles and bees [21]. Bees and pollen wasps [54] are thought to be attracted to some of the most common flower colours in *Conophytum* (e.g., pink, purple and yellow). Beetles are associated with paler colours that are much less common in *Conophytum.*

Phylogenetic structure in *Conophytum* communities

The selected *Conophytum* communities were comprised of both genetically closely related species and genetically distant species suggesting a mechanism of long-distance seed dispersal between non-contiguous populations. *Conophytum* seeds are released from the simple capsules during rainfall typically by wash-out [55]. This, however, does not explain the dispersal of seed across much larger distances, resulting in the differences in phylogenetic structure within the communities. The capsules of *Conophytum* are small, light and papery, often break off the plant [7, 13], which potentially allows for the capsules to be dispersed by wind [25, 56]. Anemochory occurs in a few genera in the Aizoaceae, including *Eberlanzia* Schwantes, *Fenestraria* N.E.Br., *Mesembryanthemum* (specifically *M.* sect. *Phyllobolus* (N.E.Br.) Klak) and *Ruschia* Schwantes [55], where the whole capsule breaks off the pedicel and is transported as a tumble fruit [17]. These tumble fruits are, however, woody and heavier [13] when compared to those in *Conophytum*, suggesting that *Conophytum* capsules could be wind dispersed across long distances. The adaptation to a long-distance dispersal mechanism has been indicated in the phylogeny and population genetics studies for the genus [14, 25]. Such dispersal events form pocket populations [57–58], which may explain the eastern expansion of *Conophytum* into the BIR (represented by Community Four). Community Four has the highest average pairwise genetic distance, as well as the largest genetic distance between species (Fig. 6B), suggesting that it includes the most distantly related species that have colonised this region through long distance dispersal events, forming a pocket population. The proposed wind dispersal mechanism may also explain the high proportion of range-restricted and point endemic species in *Conophytum*, where an adaptation in floral morphology to a newly colonised community and, without subsequent contact from closely related species, possibly forms a new species, as per the allopatric speciation model [59]. This newly formed species is therefore only found within that specific community and is thus regarded as a point endemic.

Contribution of long-distance dispersal to floral diversity in *Conophytum*

While floral diversity in a *Conophytum* community is thought to be shaped by interspecific pollination competition [12, 56], the divergence of floral traits is also related to the long-distance dispersal mechanism(s). These introduce new species that might require a different floral morphology than the other species in the community or they may be outcompeted [3, 10]. An adaptation in floral morphology may also be an adaptation to the local pollinators of the newly colonised habitat [45] or through assimilation by hybridisation [60] with local species. Without subsequent contact from other closely related species, these newly adapted species may become genetically isolated, possibly forming a new species as suggested by the allopatric species model [61–62]. This may result in different floral morphologies between closely related species found in the same community, as is suggested by the phylogenetic structure of the communities and is possibly indicative of parapatric speciation [61]. One example in *Conophytum* may be *C. ratum*, which has a highly restricted range but nevertheless two distinct forms are evident, namely a 'dwarf' summit form and a large plains form [33]. As well as the observation that diurnal and nocturnal species are nearly always sympatric [9] another feature of the genus is that a number of restricted range (point-endemic) morphologically similar diurnal species are found in temporal pairs in close proximity, but never together, separated by flowering season (e.g., *C. smorenskaduense* and *C. vanheerdei* in Community Three; and elsewhere: *C. bachelorum* S.A.Hammer and C. *confusum* A.J.Young, C.Rodgerson, S.A.Hammer & M.R.Opel; *C. brunneum* S.A.Hammer and *C. bruynsii*

S.A.Hammer, *C. youngii* C.Rodgerson and *C. rugosum* S.A.Hammer; *C. chrisolum* S.A.Hammer and *C. chrisocruxum* S.A.Hammer).

The occurrence of closely related species with different floral morphologies within a community may also be indicative of sympatric speciation [61]. This speciation model is highly controversial [63], although some studies provide strong support for it [64–65].

Habitat diversity in *Conophytum* communities

Adaptation to different niches may also separate the species in a community, especially as *Conophytum* species occupy very small habitat units due to the dwarf nature of the plants [2, 8]. A majority of species show a preference for a quartz substrate but can be found on a range of geologies, including granite, gneiss, calcrete, shale and, more rarely, on dolerite [7]. Many species-rich communities show vertical stratification of species [2, 7]. Similarly, some species show a distinct preference for a flat or very gentle slope and may therefore be found at the bottom of hills or occupying small flat patches on the top of inselbergs. The bio-climatic and habitat preferences vary across the four *Conophytum* communities and in some cases are quite broad while others are narrower (cf. Communities One and Three; Fig. 2). Species richness per se cannot always be attributed to a range of available habitats or bioclimatic conditions, as the most species-rich community, Community Two, is characterised by a single habitat type, i.e., quartz patches associated with a mountain range [66]. Similarly, the Knersvlakte, which is also comprised of different quartz patches, is regarded as a region of high species diversity and endemism in the family [13, 67–68], though not particularly so for *Conophytum* [9].

The dwarf succulent genus *Conophytum* is one of the largest in the Aizoaceae often forming diverse, species-rich communities. Such high species diversity is suggested as a possible evolutionary force driving speciation [69] and the large number of species in the genus may thus lead to further diversification. Species diversity in *Conophytum* communities is mainly explained by high floral and genetic diversity, most likely driven by the combination of interspecific competition, floral adaptation and the adaptation of wind-dispersed capsules. Species within a community are clearly separated by a combination of floral traits and genetic distance. However, differences in habitat preferences of the species adds an additional layer of complexity to each community structure. This floral and genetic separation maintains the integrity of the species within the communities. Although the pollination syndromes of *Conophytum* indicate high specialisation, the observed pollinators of the diurnal and nocturnal species seem to be relatively uniform across all the species within the respective anthesis groups. As a result, further investigation of potential pollinators of the genus is required, perhaps linking the function of the diverse floral traits to specialisation towards a specific pollinator.

96% of taxa in the genus *Conophytum* are currently regarded as being under threat of extinction (listed as Critically Endangered, Endangered or Vulnerable) [70]. This study highlights the need for conservation measures for the genus to take account of complex communities to preserve genetic diversity, rather than focusing on measures for individual species. The majority of species comprising Communities Three and Four are now included in newly designated protected areas resulting in the potential for the preservation of rich patches of species. The importance of small habitat patches for biodiversity conservation has been well established [e.g. 71, 72], especially in highly fragmented vegetation and quartz fields [73].

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Author contributions
ARM and JSB conceptualised the study; RFP collected the data; RFP, LKB and AJY analysed the data and made the figures; ARM, JSB, AJY and RFP interpreted the results and wrote the paper.

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Consent to publish
All authors approved this publication.

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