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Biodiversity and climate change: Risks to dwarf succulents in Southern Africa

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Abstract

The aim of this study was to explore the effects of anthropogenic climate change on the dwarf succulent genus *Conophytum* (Aizoaceae) within areas recognised for their floral biodiversity, namely the Succulent Karoo, Fynbos, Desert and Nama Karoo biomes of South Africa and Namibia. Niche-based modelling was used to identify the key climatic and geological variables influencing the distribution of members of the genus *Conophytum*. The distribution of the genus is primarily controlled by a small number of environmental variables, notably winter and summer rainfall levels, together with geology. Assuming a zero-dispersal model, the predicted effect of both the A1B and A2 climatic emission scenarios was a severe contraction in the area satisfying the bioclimatic envelope for the genus coupled with significant range dislocation. Reductions of >90% in suitable habitat for 10 of the 16 taxonomic Sections that comprise the genus and represent >80% of taxa under the A2 scenario are predicted. Under A1B the projected effects are ameliorated, but reductions of >50% of habitat can be seen in a majority of Sections. Significant projected reductions in the habitable bioclimatic envelope are very likely to increase risk of extinction of ~80% of taxa even under a partly mitigated emissions scenario.

1. Introduction

Anthropogenic climate change is recognised as one of the main potential threats to biodiversity over the course of this century. Early projections indicated that richly bio-diverse regions including the Succulent Karoo and Fynbos biomes of southwestern Africa would be particularly prone to predicted changes in the climate (e.g., Midgley et al., 2002, 2006; Midgley and Thuiller 2007). More recently a report by the South African Department of Environmental Affairs (DEA, 2014) has instead predicted a more complex suite of changes across the various biomes of the region, with potential expansion of some (e.g., Desert) and contraction of others (e.g., Fynbos). Contrary to the results of earlier studies, the area that lies within the climatic envelope of the Succulent Karoo biome is now thought to largely persist under all climate scenarios tested, through to 2050, with higher risks of extinction contingent on continued warming. While the inherent richness in floral diversity, especially amongst succulents, is one of the defining elements of the region, such diversity makes the prediction of responses to environmental change (e.g., increasing aridity and thermal stress) challenging. For example, the variability amongst the flora of these biomes in terms of drought tolerance is thought to be especially significant (e.g., Hoffman et al., 2009).

Lying within the southwestern corner of Africa, the Succulent Karoo biome is recognised as one of the most important regions of floral biodiversity globally (Mittermeier et al., 1998, 2004). The biome is an area of approximately 116,000 km^2 lying on the fringes of the Cape Floristic Region. It is characterised by a low winter rainfall (Desmet and Cowling 1999a; Jürgens 1991, 1997; Rutherford and Westfall, 1994) and is regarded as one of only two global biodiversity hotspots that are fully arid (Cowling et al., 1998; Mittermeier et al., 2004). The primary climatic factors affecting the biome are temperature and precipitation (rainfall, fog and dew) both in amount and seasonality. Rainfall declines east to west and south to north but is also characterised by its unpredictable nature. Non-rainfall moisture is thought to make a significant contribution to make a substantial, and reliable, contribution to total moisture availability (Matimati et al., 2013). Fog is recognised to be especially prevalent on the west coast and along some larger river systems, notably the Orange River. The contribution made by dew to annual precipitation appears to be less pronounced (<20-fold

less), although it is much more widespread than the effects of fog (Matimati et al., 2013). 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 particular climatic conditions within the Succulent Karoo lead to a unique flora, dominated by a large number of leaf succulents, especially members of the Aizoaceae and Crassulaceae (Cowling and Hilton-Taylor, 1999; Jürgens 1991, 1997). The biome is strongly species-rich, with approximately 5,000 vascular plant species recorded, and displays high floral endemicity (~40%). The miniaturisation of growth form in leaf succulents (as seen in the genus *Conophytum*) is an adaptation especially evident in the Succulent Karoo (Desmet and Cowling, 1999b). Within the Aizoaceae a high degree of speciation is evident (Klak et al., 2004), no more so than in the miniature or dwarf succulent genus *Conophytum,* which has >160 recognised species and subspecies (Hammer and Young 2016). Young and Desmet (2016) determined that more than half (96) of all *Conophytum* species and subspecies are endemic to the Succulent Karoo biome alone with >90% of all *Conophytum* taxa found within this single biome. Members of the genus are found in all six bioregions that comprise the Succulent Karoo in South Africa, and display a particularly strong association with the Namaqualand Hardeveld and Richtersveld bioregions. Within Namibia, the genus is also most closely associated with the biome. Within the Succulent Karoo, the highest levels of floral species diversity, especially in dwarf succulents, are often associated with koppies or rocky outcrops (Desmet and Cowling, 1999b). The flora of the biome is also characterised by high levels of point (local / range-restricted) endemism (Cowling and Hilton-Taylor, 1994; Driver et al., 2003; Mucina et al*.,* 2006). Such point endemism is most pronounced amongst succulents, especially members of the Mesembryanthemacae, including *Conophytum* in which more than one fifth of all taxa can be considered point endemics (Young and Desmet, 2016). The range distribution of the genus *Conophytum* lies predominantly within a winter rainfall area with a few taxa extending, through a precipitation transitional zone, east into the Bushmanland and Griquland Nama Karoo (areas with summer rainfall). The vast majority (93%) of taxa are associated with the Succulent Karoo (especially the Namaqualand Hardeveld and Richtersveld bioregions) and the Desert biomes (Young and Desmet, 2016). Substantially fewer taxa are found within the Fynbos and Nama Karoo biomes. The strongest

affinity of the genus is with the Namaqualand Hardeveld bioregion which is home to 84 taxa alone, including 43 that are endemic to that single bioregion.

While predictions of the possible effect of climate change on individual biomes now exist (e.g., DEA 2014) there are few studies exploring such effects on individual plant genera. Until now one of the major restrictions in performing such analyses has been the lack of accurate locality data for succulents. These represent a key element of the flora of the region, all the more so as they are recognised as amongst the best-adapted plants to the local environmental conditions, especially drought tolerance (e.g., Musil et al., 2010). Utilising a comprehensive location database, the aim of this study was to assess the vulnerability of the dwarf succulent genus *Conophytum* to anthropogenic climate change in this region.

2. Methods

2.1 Vegetation data

This study concerned the dwarf succulent genus *Conophytum* at species and subspecies level as defined by Hammer and Young (2016). The genus consists of 165 recognised species and subspecies, of which the localities of just six are currently unknown (lost or possibly extinct in habitat). Distribution of taxa was represented by the locality data in >2,700 points, mainly the result of fieldwork conducted by two of the authors (Young and Desmet, unpublished data). The recorded locality data were carefully assessed for error before using them in the model and where accurate gps recordings were not available, distributions were individually geo-referenced to within 0.5km of their stated location. When this was not possible or in cases when the identification of the taxon was uncertain, data was excluded from this study. The vast majority of all available data arise from South Africa and much less from Namibia. Nevertheless, all available records were used as long as the accuracy of the record was deemed sufficiently rigorous. In addition to studying the effects on the genus *Conophytum*, the potential effects of the chosen emission scenarios (see below) were modelled on closely related groups of *Conophytum* species and subspecies organised into discrete taxonomic Sections, based on their morphology (as recognised by Hammer, 2002 and Hammer and

Young, 2016). The adoption of Sections here allows the combining the locality records for several taxa and therefore permits the inclusion of those species and subspecies for which there are only a limited number of locality records (i.e., where either the number of known localities is low or for taxa which are point-endemics and are severely range-restricted).

2.2 Global emission scenarios

The climate and environmental data used were from the Worldclim database (Hijmans et al., 2005), and from the National Land-cover Project 2006. To examine the possible future climate change impacts on the geographic distribution and potential range shifts for the genus *Conophytum* in southern Africa, projected future (2040-2069) climate data (Ramirez and Jarvis, 2008) were used with the present (1950-2000) climate data, with a resolution of 1 km x 1 km. ECHAM5 is the fifth generation of the ECHAM general circulation model, and it is a global climate model developed by the Max Planck Institute for Meteorology (Roeckner et al., 2003). It was specifically adjusted by modifying global forecast models developed by the European Centre for Medium-Range Weather Forecasts, so that it can be used for climate research. ECHAM5 and other global climate models were recently used in the IPCC Fourth Assessment Report, where it proved to be a reliable global climate model by comparison to others (e.g., Connolley and Bracegirdle 2007). MIROC (considered to be the wettest global climate change scenario), ECHAM5 (an intermediate rainfall future) and CSIRO (driest) were initially evaluated in our studies. ECHAM5 was chosen as it was seen to be better suited for predictions of Southern Africa climate, with its inherent regions of dryness and wetness. ECHAM5 has also used by the recent analysis of climate change in the studies for the South African Department of the Environment (DEA, 2014).

In this study, the impact of climate change was examined under two different carbon emission scenarios. Potential changes in the future on the distribution area of the 16 Sections that comprise the genus compared to the present distribution were analysed. To explore how sensitive *Conophytum* may be to climate change, the A2 and A1B climate scenarios were used to allow between-model comparison, assuming unconstrained and constrained global fossil fuel emissions, respectively. The A2 climate scenario (as used by DEA, 2014) assumes self-reliance, preserving local identities, with moderate regional

economic development, but with a high increase in population, increased resource utilisation, a slower technological development and higher CO_2 emissions (Parry et al., 2007). The A1B climate scenario assumes rapid economic growth resulting in a global population that peaks mid-century and declines afterwards, combined with a more rapid development of efficient technologies, reducing the reliance on selected energy sources (Parry et al., 2007). These two scenarios were not used as absolute possible scenarios for the future, but more as a tool to explore the sensitivity of the genus *Conophytum* to predicted changes in climate in the future. The A2 scenario is in line with current emissions trends (Nakicenovic et al., 2000), while the A1B scenario adopts a slightly more mitigated emissions pathway.

The effects of scenarios A1B and A2 on the geographic range of the genus in South Africa and Namibia were modelled using MaxEnt (Phillips et al., 2004, 2006). This applies Bayesian methods to estimate the potential geographic distribution of species by finding the probability distribution of maximum entropy and is an effective method for modelling species distributions from presence-only data. This spatial modelling software can also address sampling bias that is common in geographical records because collections usually favour the most accessible areas (e.g., close to roads and within nature reserves), thus making it a suitable tool for the present study. The first stage was to relate current environmental conditions to occurrence data for the 16 recognised Sections that comprise the genus *Conophytum* and subsequently made spatial predictions for the two climate change scenarios. The conventional Bayesian risk criterion is based on the quadratic loss function and use of a conjugate family (Guo, 2010), and the Maximum Entropy modelling is an important Bayesian inference, which is established by different risk criteria. In this case the species distribution probability is statistically estimated by searching the family of probability distributions under the maximum entropy criterion subject to environmental constraints.

The species distribution projections used in this study used Gibbs sampling. This is a statistical algorithm used by Bayesian inference. The Gibbs family {$q_\lambda(x)$, $\lambda \in L$} is expressed as follows:

$$q_\lambda(x) = \frac{1}{Z_\lambda(x)} \exp\left(\sum_{i=1}^{m} \lambda_i f_i(x) \right)$$

eq. 1

where $\lambda_i = (\lambda_1, \lambda_2, ..., \lambda_m)$ is the weight vector, λ_i represents the weight parameter, L is the m-dimensional space, $f_i(x)$ represents the probability distribution of species i, and $Z_\lambda(x)$ is the normalised constant. Note that each element x is a pixel in the investigated area. The probabilities $f_i(x)$ represent the relative suitability of the environmental conditions in each pixel (Philips et al., 2004, 2006; Elith et al., 2011).

2.3 Environmental variables

In order to explore the bioclimatic envelope of the genus *Conophytum*, a total of 20 environmental variables were explored at a resolution of 1km. These consisted of 16 bioclimatic variables together with four separate variables reflecting geology (substrate). The choice of variables adopted for the study reflected the main climatic factors affecting the Succulent Karoo as identified by Desmet and Cowling (1999a). The climatic variables used were: maximum and minimum temperatures (T_{max}, T_{min}, respectively), average temperature and rainfall (T_{av} and $P_{av,}$) for all four seasons. Seasonal periods were defined as: Q1 = December, January, February; Q2 = March, April, May; Q3 = June, July, August; and, Q4 = September, October, November. A number of environmental variables were adopted as possible constraints on the potential for migration or dispersal events by *Conophytum* taxa. These were comprised of: altitude (elevation above sea level in meters), terrain morphology (plains, slopes), geology 1 (igneous, limestone, quartzite, sand, schist, shale, ultramafic) and geology 2 (acidity, alkalinity). The full range of environmental variables used is given in the Appendix.

Each spatial model generates the percentage contribution for every predictor variable used with a percentage contribution being estimated from the iterations of the training algorithm by adding or subtracting regularized gain to the variable in question. Modelling was performed using default parameters, with regularization multiplier = 1, maximum iterations = 500 and the random test percentage of 20%. Model performance was determined by area under curve (AUC) of the training and test data for the genus and individual Sections (see Fig. 1 for abbreviations): BAR (AUC = 0.980), BAT (AUC = 0.992), BIL (AUC = 0.982), CAT (AUC = 0.968), CHE (AUC = 0.975), CON (AUC = 0.963), COS (AUC = 0.971), CYL (AUC = 0.986), HER

(AUC = 0.987), MIN (AUC = 0.973), OPH (AUC = 0.981), PEL (AUC = 0.986), SAX (AUC = 0.980), SUB (AUC = 0.991), VER (AUC = 0.987), WET (AUC = 0.973). The average AUC taken across all Sections was 0.979, indicating an excellent predictive ability of the models.

A habitat was considered suitable for *Conophytum* if the probability of persistence was ≥0.3 while regions with a probability <0.3 were assumed to be unsuitable for long-term survival. Two plots of [omission vs. predicted area] and [sensitivity vs. specificity] were generated and a calculation of model performance were used to determine the persistence threshold for each *Conophytum* Section. In this case, a threshold of 0.3 that maximized both training sensitivity and specificity under the current climate (Liu et al., 2005) was adopted.

3 Results

3.1 Present (1950-2000)

In this study, response curves generated by the spatial modelling software show that the distribution of *Conophytum* is predominantly influenced by two main environmental variables, namely geology and the amount of rainfall in the warmest quarter, Q1 (see Appendix; the amount of rainfall is equivalent to 5-35mm of precipitation). The warmest quarter (Q1) coincides with the natural dormancy period of the genus, with growth and, in the vast majority of taxa, flowering being most prevalent in the autumn months (Q2). Other important variables influencing the distribution range of members of the genus are the minimum temperature and rainfall within the coldest quarter (Q3), and rainfall within Q2.

When explored at Section level within the genus, geology was found to be the dominant or at least a significant factor in a majority of Sections (except Biloba, Conophytum, Minuscula, Saxetana, Subfenestrata and Wettsteinii). Rainfall within the warmest and / or coldest quarters was a significant environmental factor for all but three sections (Herreanthus, Ophthalmophyllum and Verrucosa). Taxa in Sections Ophthalmophyllum and Verrucosa are somewhat geographically disjunct from the rest of the genus and primarily occupy the northern part of the Bushmanland bioregion in the Nama Karoo biome (lying to the east of

the town of Springbok and south of the Orange River) and the easternmost fringes of the Namaqualand Hardeveld bioregion. This area lies within the transitional zone for winter-summer rainfall.

3.2 Projected future (2040-69) scenarios

The projections for both emission scenarios (A1B and A2) show a potential range shift of members of the genus coupled with significant habitat fragmentation (Figs. 1-2). In each case, the projections are presented assuming both a full (universal) migration or perfect dispersal model (allows for 'positive change' in Figs. 1-2) and a, more realistic, zero-migration model (ignores 'positive change' in Figs. 1-2). Assuming full migration, *Conophytum* would appear to be reasonably well-adapted to future climatic conditions, and exhibited a theoretical potential for range expansion. However, the predicted loss of existing suitable habitat across the genus was determined to be 70.5% and 33.8% under scenarios A2 and A1B, respectively. The potential for habitat expansion under both scenarios this would be hampered by both geographic range shift (e.g., in Section Batrachia of 200-600km distant from existing locations, depending on the scenario) coupled with habitat fragmentation (Figs. 1-2). The most striking overall effect is a marked potential range expansion for the genus to the east and northeast into southern Namibia. Under scenario A1B a further concentration of suitable habitat is seen in the Succulent Karoo in the southwestern corner of Namibia, along the Orange River and into the southern Sperrgebiet (Fig. 1). The A2 model, by contrast, suggests the potential for a massive expansion of range north towards the coastal town of Luderitz into the Namib Desert and east through the Bushmanland bioregion in the Nama Karoo biome (Fig. 2). The predicted range shift of the genus through the Ganka Karoo to the southeast of the current distribution is also marked.

Each taxonomic Section responded differently to each emissions scenario in terms of potential habitat gain and loss of current suitable habitat (Figs. 1-2). For example, Sections Cylindrata and Subfenestrata exhibited the lowest loss of habitat under emissions scenario A1B, yet the relative importance of the environmental variables tested in this study were very different (geology is of primary importance in the former, while summer rainfall is key in the latter). A number of Sections are currently highly geographically localised (e.g., Section Costata) while others occupy a very large range (e.g., Section Minuscula). Such differences in

current distribution range do not, in themselves, necessarily reflect subsequent responses to climate change. There was no clear pattern between predicted habitat loss or gain across the different Sections, i.e., a large value for habitat loss does not always equate to a low gain. However, those Sections such as Cataphracta, Cylindratum and Batrachia (in the Succulent Karoo biome) appeared to be well buffered against habitat loss under emission scenario A1B (but not under A2). Differences in the response of Section Costata to A1B (55% habitat loss) and A2 (3% loss) are not understood and rather contradictory to the behaviour seen in the other Sections.

Assuming a zero-dispersal model, both scenarios would result in a severe contraction in the bioclimatic envelope for the genus (Fig. 3), with reductions of >90% in current habitat for 10 of the 16 Sections predicted under the A2 scenario (Fig. 3B), with all others (except Section Costata which consists of just two taxa) would experience a reduction of >68% in current habitable land. The vulnerability of *Conophytum* to both emission scenarios is shown in Figure 4. Under A1B more than half of all *Conophytum* species and subspecies would see a loss of >50% currently suitable habitat, with 43% experiencing a loss of 70% or more. Under scenario A2 the effects are more drastic, with >90% of *Conophytum* taxa predicted to lose 70% or more of their current habitat. The risk of extinction is high, with more than 90 of the 160 taxa predicted to lose >90% of their existing habitat (Fig. 4).

The zero-dispersal model shows that the Succulent Karoo biome will remain the main centre for the genus and will essentially define the future range for most surviving taxa (especially the Namaqualand Hardeveld bioregion).

4. Discussion

The dwarf succulent genus *Conophytum* is one of the largest in the Aizoceae and generally regarded as one of the most adaptive of the dwarf succulents as it occupies such a wide geographical range and geologies. It is also one of the largest of the genera present in the Succulent Karoo biome. Such dwarf succulents are thought to be amongst the most resilient of plant species in the biome to environmental change. By contrast both therophytes and geophytes show increased sensitivity to both drought and temperature extremes (Hoffman

et al., 2009). Both emission scenarios examined in this study predict changes in the bioclimatic envelope for members of the genus. Both the A1B and A2 emission scenarios tested in this study result in pronounced habitat fragmentation and range dislocation for the genus (Figs. 1-2). However, there are marked differences in the response of different Sections to the two emission scenarios. While loss of habitat is less pronounced under A1B compared to A2, the potential for range expansion (assuming effective dispersal) is also reduced. Overall, the study indicates that the potential loss of current habitat for the vast majority of members of the genus *Conophytum* will be in the range 50-100%.

Midgley et al. (2002) proposed a link between range dislocation and extinction potential in the Fynbos as the predicted rate of climate change is likely to exceed the ability of populations to migrate (as limited by dispersal mechanisms, for example). While the potential for dispersal or migration as a whole in *Conophytum* is very poorly understood these conclusions are equally applicable here. Migration rate assumptions in the order of 1-5km per decade have been used in other floral studies (e.g., Midgley et al., 2006), with the lower limit (arguably an over-estimation) reflecting ant or rodent-aided dispersal and the higher value for wind-borne dispersal events. While the seed capsules for *Conophytum* taxa are small and light they are not specifically adapted for wind-dispersal. Coupled with the fact that the capsules are also very fragile (mitigating against longer-distance travel) it is reasonable to assume that a maximum rate of 1 km per decade could be applied. This contrasts, however, with the estimates of range dislocation for individual *Conophytum* Sections from this study, which are in the range of tens to hundreds of kilometres. Such large dislocations will clearly be a major limiting factor in the subsequent potential for the genus to migrate to other suitable habitats, and likely only overcome through human intervention (assisted migration). While a partial dispersal model has not been run for this data, it is suggested that the results assuming a zero-dispersal approach will be most appropriate and better indicates the risk for extinction (Fig. 3). Known occurrences of colonisation by *Conophytum* taxa in recent timescales are rare, with perhaps the best-known example being that of *C. luckhoffii* on the vertical cuttings made in 1958 at Piekeniers Pass in the Western Cape region of South Africa. In this instance established populations of *C. luckoffii* have been recorded from within ~2-3km of the cutting so the distances involved in such colonisation are much less than those indicated by the modelling here. It is also worth

noting that the few attempts at recolonisation through seed dispersal have not met with success in this genus (S.A. Hammer pers. comm).

Bellard et al. (2014) predict a loss of approximately one third of all endemic species within the Succulent Karoo (819 species) due to climate change under emissions scenario A1. The data here suggest that dwarf endemics such as *Conophytum* may be especially vulnerable to such change, despite the fact that experimental studies have suggested that such dwarf succulents may be amongst the most well adapted to drought (e.g. Musil et al., 2010). The models predict a substantial range reduction (i.e., loss of currently suitable habitat) for the majority of *Conophytum* taxa, especially under scenario A2. Even under the more moderate A1B scenario more than half of all *Conophytum* species and subspecies would experience a reduction in current habitable range of more than 50%. The high incidence of point-endemism within the genus further exacerbates the risk of extinction.

The current spatial distribution in *Conophytum* is strongly influenced by geology (see Appendix) and the availability of suitable substrate will be a powerful influence on the potential range shift of individual members of the genus. Driver et al. (2003) highlighted the potential that the quartz fields of the Knersvlakte present for species migration and the importance of quartz fields within the Succulent Karoo biome has been highlighted by Schmiedel and Jürgens (1999). Given the potential effects on *Conophytum* distribution shown in this study these quartz corridors could prove to be a major factor in mitigating the effects of range dislocation, all the more so given the lack of suitable substrate on the sandstone-dominated landscape of the Bokkeveld Plateau to the southeast and granite/gneiss to the east and north of the Knersvlakte. Such 'geological gaps' will in many areas where *Conophytum* is prevalent further inhibit longer-distance migration (e.g., in the inselbergs of Bushmanland).

Topographic diversity has been identified as having a buffering effect moderating the potential effects of climate change (e.g., in the case of Fynbos biome; Midgley et al., 2002) and can form part of a conservation strategy (Halpin 1997). In the genus *Conophytum,* the data presented here suggest that this does not appear to be the case – altitude is not a significant factor in the distribution of the genus, with taxa thriving in both coastal areas at

sea level and in some of the highest mountain regions such as the Khamiesberg. It is probable that the potential amelioration effect afforded by altitude is outweighed by the overwhelmingly deleterious effects of climate change.

As with many other dwarf succulents (Ihlenfeldt, 1994; Desmet et al., 1998), the genus *Conophytum* is characterised by a high degree of speciation and endemism. While a small number of the 159 species and subspecies studied here may be found occupying a very large latitudinal range (e.g., *C. bilobum* and *C. pageae*) most are much more heavily restricted in their distribution within the overall bioclimatic envelope for the genus. Indeed the potential impact of climate change is compounded by the number of highly localised, point endemics seen in the genus. Such point endemics account for ~28% of all *Conophytum* taxa and are especially prevalent within the Succulent Karoo biome (Young and Desmet, 2016). Opportunities for migration among such habitat specialists would be expected to be considerably reduced compared to more widespread taxa. Such taxa are especially vulnerable to climatic or other environmental or human-made changes (e.g., expansion of mining and fracking activities). Members of the genus display a range of growth forms but this does not appear in itself to be a factor in determining how individual taxa respond to climate change. For example, those taxa which can be described as a subterranean form of nanochamaephytes (see Schmiedel and Jürgens, 1999), especially those in Section Ophthalmophyllum, overall behave very similarly to other taxa in response to climate change under both emission scenarios.

This study can assist in future planning in identifying and managing areas of conservation potential within the bioclimatic envelope occupied by the genus *Conophytum* now and into the future. Less than one third of *Conophytum* taxa occur within current formal protected areas within South Africa and Namibia (Young and Desmet, 2016). These formal conservation areas do not however align well with the predicted distributions of taxa under either the A1B or A2 emission scenarios. However, some of the areas identified in South Africa under the National Protected Areas Expansion Strategy (NPAES focus areas) have the potential to provide more comprehensive coverage of taxa given the projected future distributions, especially under the A1B emissions scenario. The Knersvlakte bioregion is one of those most adversely affected under both emission scenarios (especially A2) and is of

particular significance within Southern Africa in terms of its biodiversity (leading to its designation as a Nature Reserve in 2014). The quartz fields of the Knersvlakte are home to several *Conophytum* taxa, including *C. acutum*, *C. minutum*, *C. subfenestratum* and *C. uviforme. C. uviforme* ssp. *subincannum* uniquely inhabits limestone and several other species are found on the periphery of the area (e.g., *C. reconditum*). The predicted range of these taxa, with the exception of *C. subfenestratum*, will be greatly reduced under the conditions predicted by emission scenario A1B and completely lost under scenario A2. Schmiedel et al. (2012) suggest that in the quartz-field populations of the Knersvlakte the 'near-endemic and habitat-specialised' plants may be better buffered against variation in annual rainfall patterns than previously thought. Here, the influence of other sources of moisture such as dew and localised fogs may be significant in plant survival (Matimati et al.*,* 2012). However, it is not known how such localised events may be influenced by the emission scenarios studied here. The results of passive warming experiments in the Knersvlakte indicate that quartz field species are already close to their limits of thermal tolerance (Musil et al., 2009, 2010).

The results suggest that the Namaqualand Hardeveld bioregion within the Succulent Karoo biome will remain (see Young and Desmet, 2016) the single most important geographical area for the genus under both emission scenarios. Key areas include the Namaqualand Klipkoppe Shrubland (currently the single most diverse vegetation unit for the genus with 67 taxa, including 23 endemic to the vegetation unit) and Namaqualand Heuweltjieveld vegetation units. The AIB climate model indicates that Richtersveld bioregion will also remain an important centre for members of the genus, especially the Lekkersing Succulent Shrubland (12 taxa) and Southern Richtersveld Inselberg vegetation units (11 taxa).

5. Conclusions

Overall, the risk of extinction to a majority of species and subspecies of the genus *Conophytum* as a result of climate change is extremely high. These deleterious effects are likely compounded by the high degree of point endemism seen in this genus, a trait shared with some other succulent genera. Such results are of special concern for the wider floral composition of the region's biomes, especially the Succulent Karoo where *Conophytum* is

most prevalent, as it is generally recognised that dwarf succulents such as *Conophytum* are amongst the best-adapted plants to drought. As a recognised global biodiversity hotspot, the impact of climate change on the floral diversity of the Succulent Karoo biome is therefore of special concern. The data here indicate that although the overall climate envelope of this biome may not change significantly as a result of climate change (DEA, 2014), the effect on individual genera and species that occupy the biome may be profound. The potential vulnerability of the Succulent Karoo (together with the Horn of Africa, Madagascar, the Indian Ocean islands, and the mountains of southwest China) to land use change has been highlighted recently by Ballard et al. (2014), who suggested that at least 20% of herbaceous cover may be lost. This would further increase the risk of loss of biodiversity and enhance the risk of extinction in the biome. Currently, few conservation strategies properly take into account climate change, focusing instead on changes in land use or reclamation. The results of our modelling suggest that conservation strategies and planning for the Succulent Karoo and adjacent biomes should consider the results of climate change modelling , identifying those areas both at highest risk and those that would appear to be most resilient to and can buffer against such changes.

Appendix A. Supplementary data

The following are the supplementary data relating to this article

Table S1. Predicted change in suitable land area for sections of the genus *Conophytum*

Table S2. List of species in the genus *Conophytum* as recognised by Hammer and Young (2016). Locality data for all the taxa listed was used in the climate change modelling except for *C. semivestitum* and *C. herreanthus* ssp. *herreanthus* which are both lost in habitat. Natural hybrids were excluded from the study as was any collection of uncertain taxonomy.

Fig. S3. Sample locations of *Conophytum* in Namibia and South Africa.

Table S4. Contribution of variables for the present distribution of *Conophytum* Sections.

Fig. S5. Photographs of *Conophytum* taxa in habitat. A. *C. turrigerum* is a habitat specialist known from fewer than ten sites where it grows in lichen and moss on granite - here at Paarl, Western Cape, South Africa; B. *C. marginatum* ssp. *littlewoodii* in habitat in the Northern Cape, South Africa. This taxon is restricted to four known sites within South Africa, all close to the Orange River in northern Bushmanland; C. One of the smallest members of the genus, *C. rugosum* growing in a grit pan on gneiss in the Northern Cape, South Africa. This type of habitat is preferred by a wide range of *Conophytum* taxa and is particularly vulnerable to disturbance; D. *C. subterraneum* is a quartz field specialist that is only recorded from a single site in the Richtersveld, Northern Cape, South Africa.

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Figure legends

Fig. 1 Projected changes in the geographic range for individual Sections of the genus *Conophytum* under the A1B emissions scenario: (A) Sections Batrachia to Cylindrata; (B) Sections Herreanthus to Wettsteinia. The red dots indicate current locations for *Conophytum* taxa within each taxonomic Section. Abbreviations: BAR Barbata; BAT Batrachia; BIL Bilobum; CAT Cataphracta; CHE Cheshire-Feles; CON Conophytum; COS Costata; CYL Cylindrata; HER Herreanthus; MIN Minuscula; OPH Ophthalmophyllum; PEL Pellucida; SAX Saxetana; SUB Subfenestrata; VER Verrucosa; WET Wettsteinia (see Hammer, 2002).

Fig. 2 Projected changes in the geographic range for individual Sections of the genus *Conophytum* under the A2 emissions scenario: (A) Sections Batrachia to Cylindrata; (B) Sections Herreanthus to Wettsteinia. The red dots indicate current locations for *Conophytum* taxa within each taxonomic Section. See Fig. 1 for abbreviations.

Fig. 3 Predicted land area changes for the recognised sections of the genus *Conophytum* under emission scenarios (A) A1B, (B) A2. See Fig. 1 for abbreviations.

Fig. 4 The vulnerability of taxa (to subspecies level) in the genus *Conophytum* to climate change under emission scenarios A1B (🟦) and A2 (🟥). The loss of existing suitable habitat has been used as a measure of the potential impact of climate change on a taxon assuming a zero-migration model (assumed here to be most appropriate).
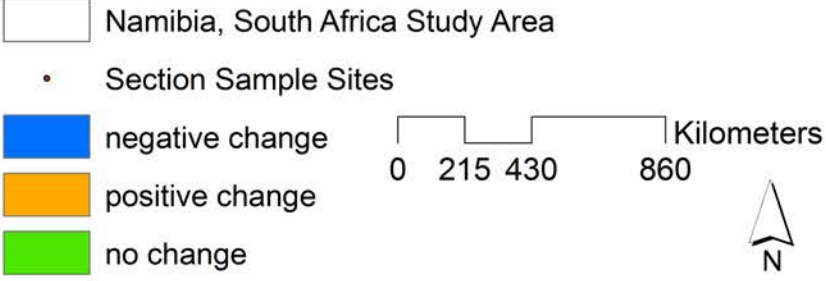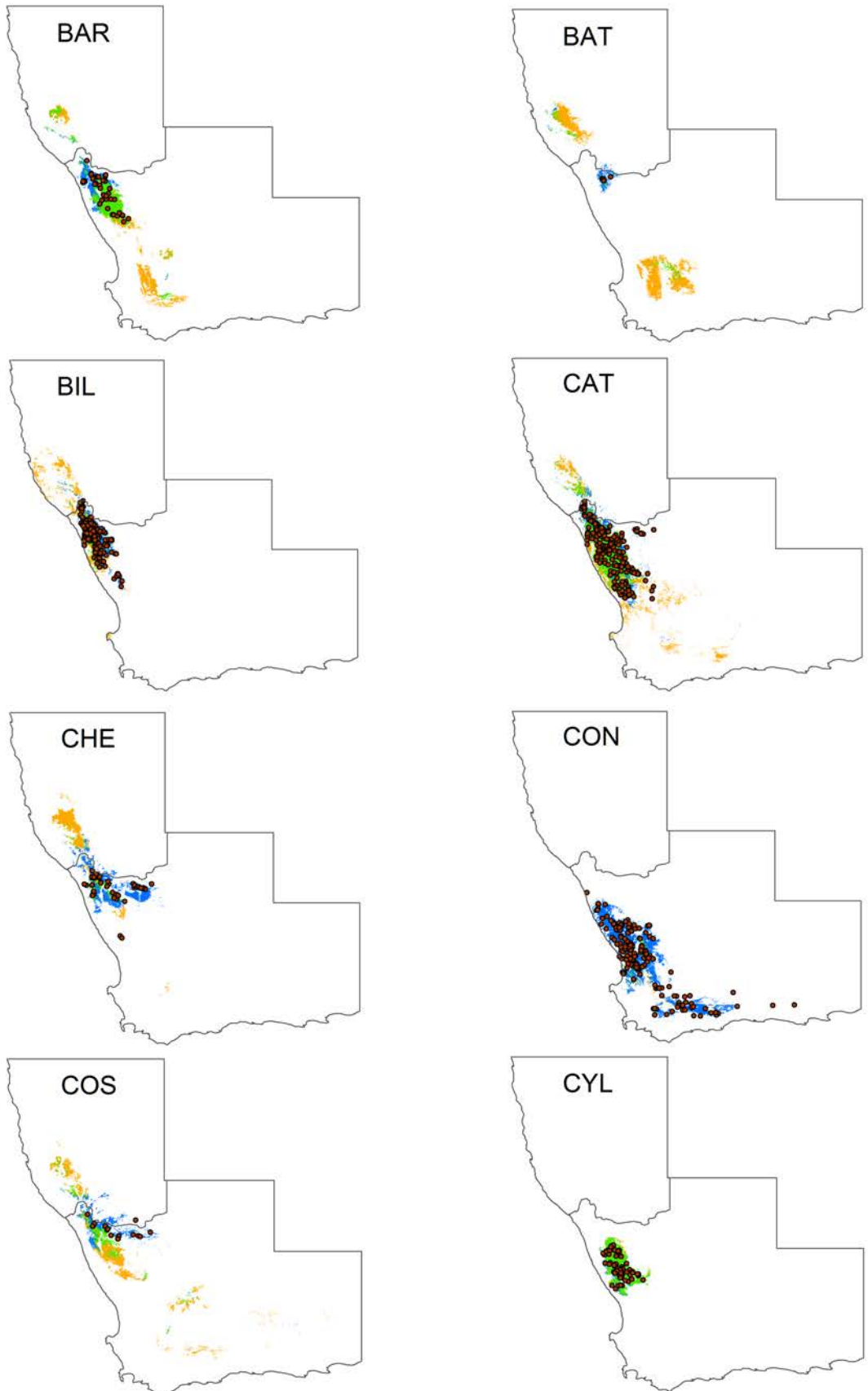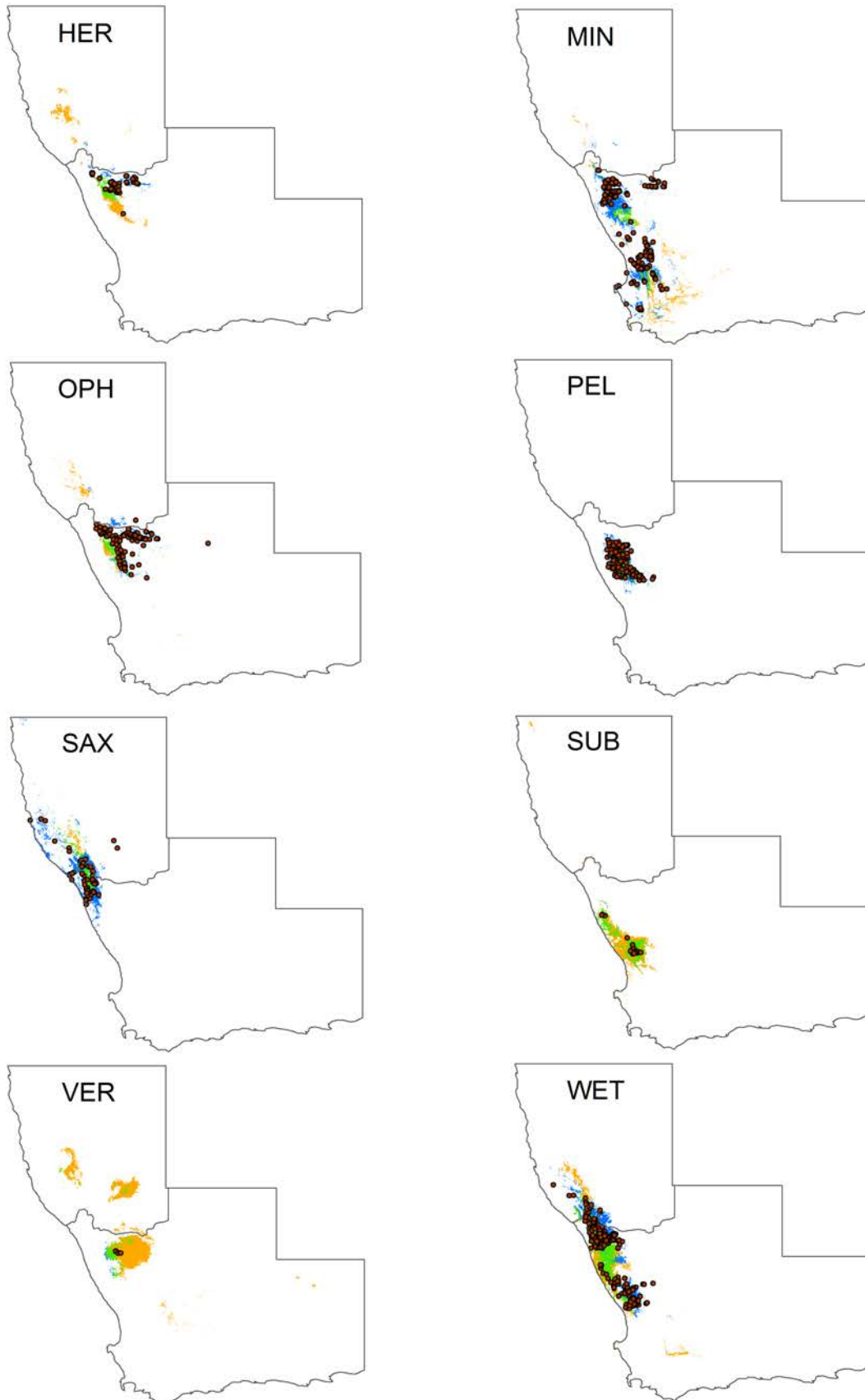
BAR

BAT

BIL

CAT

CHE

CON

COS

CYL

Namibia, South Africa Study Area

• Section Sample Sites

negative change

positive change

no change

Kilometers

0   215 430   860

N

HER

MIN

OPH

PEL

SAX

SUB

VER

WET

Namibia, South Africa Study Area

•   Section Sample Sites

negative change

positive change

no change

Kilometers

0   210 420   840

N

BAR

BAT

BIL

CAT

CHE

CON

COS

CYL

Namibia, South Africa Study Area

• Section Sample Sites

negative change

positive change

no change

Kilometers

0   215 430   860

N

HER

MIN

OPH

PEL

SAX

SUB

VER

WET

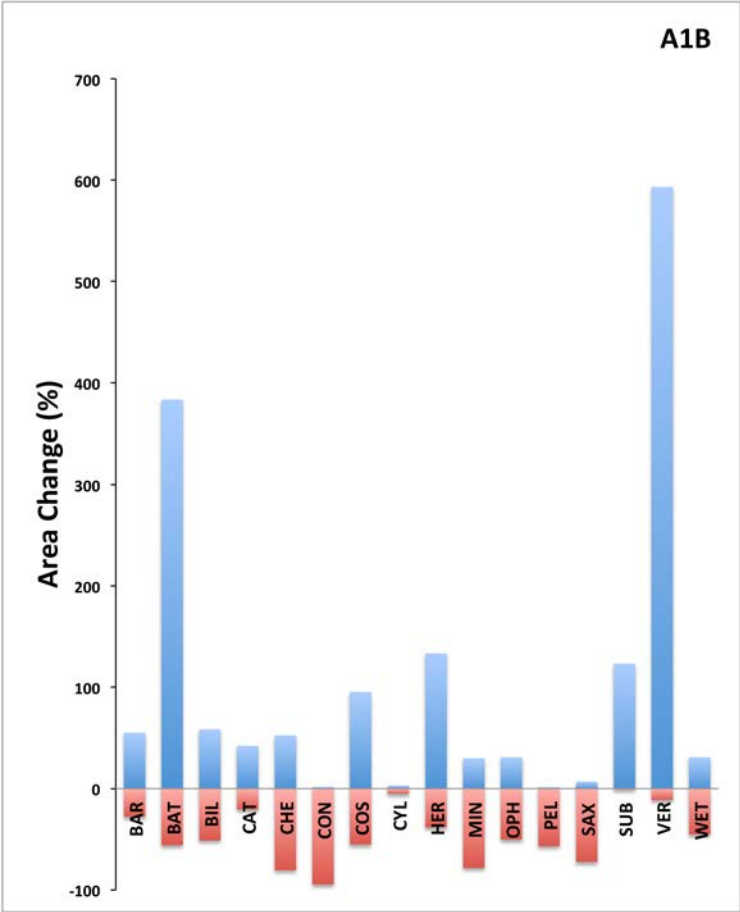Namibia, South Africa Study Area

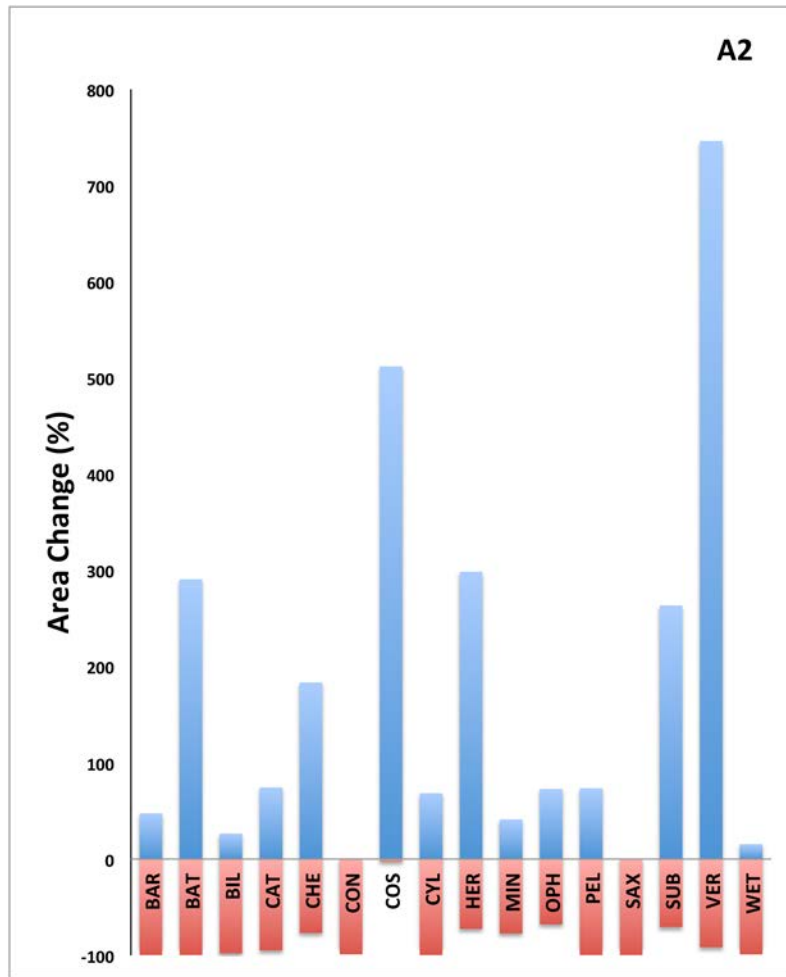•   Section Sample Sites

negative change

positive change

no change

Kilometers

0   225 450   900

N
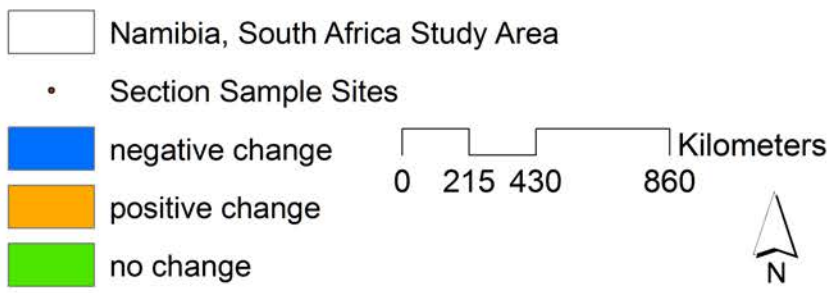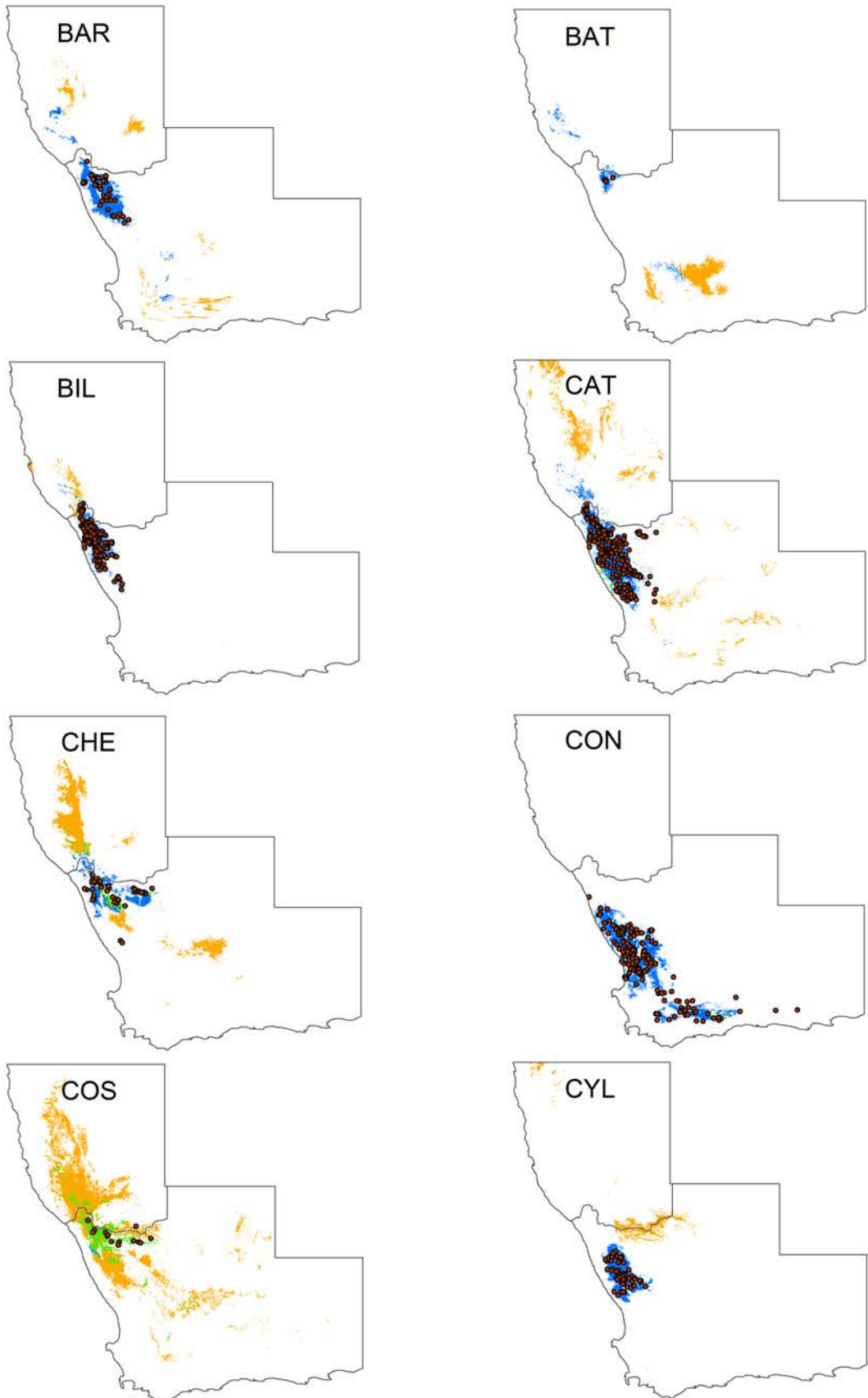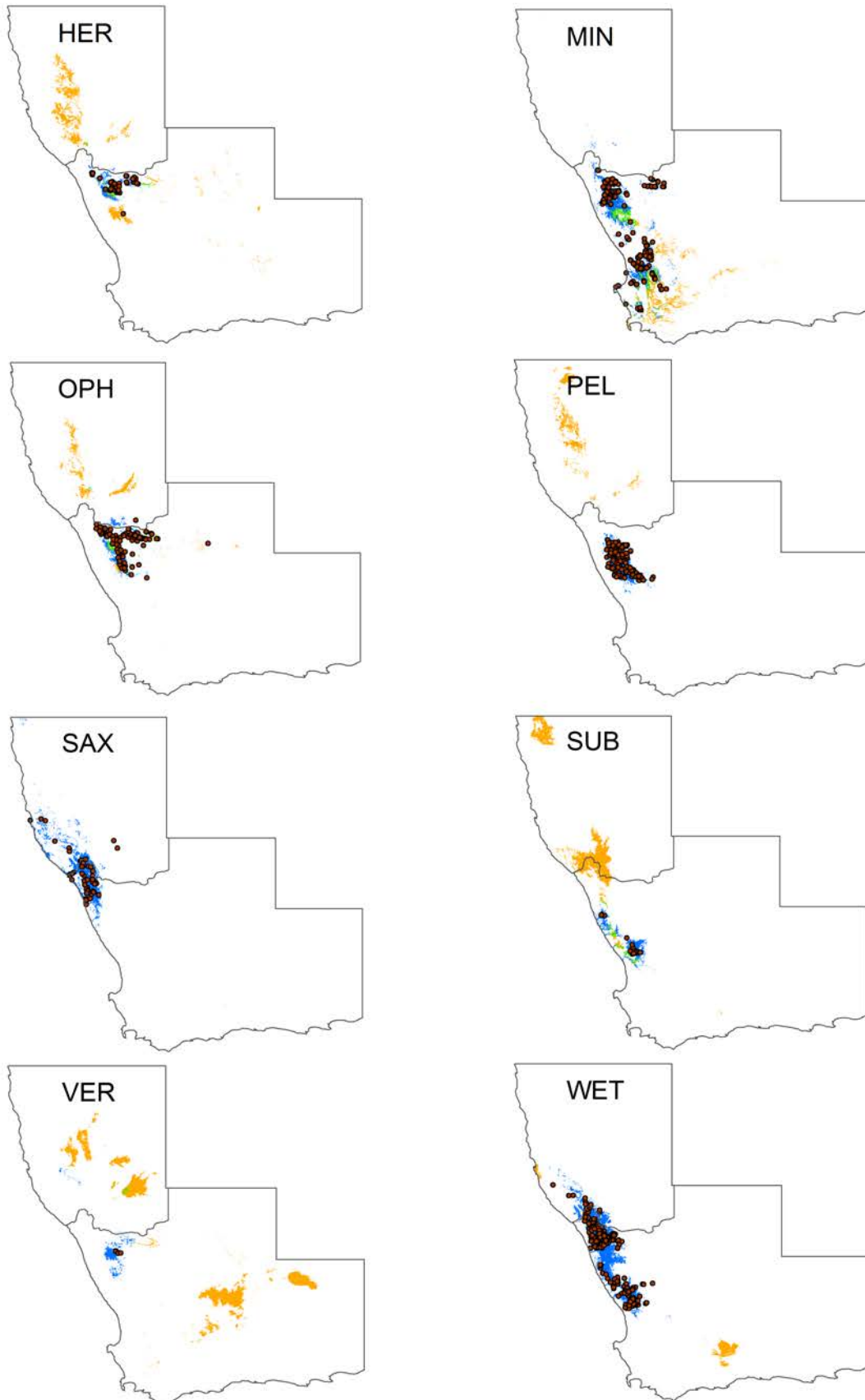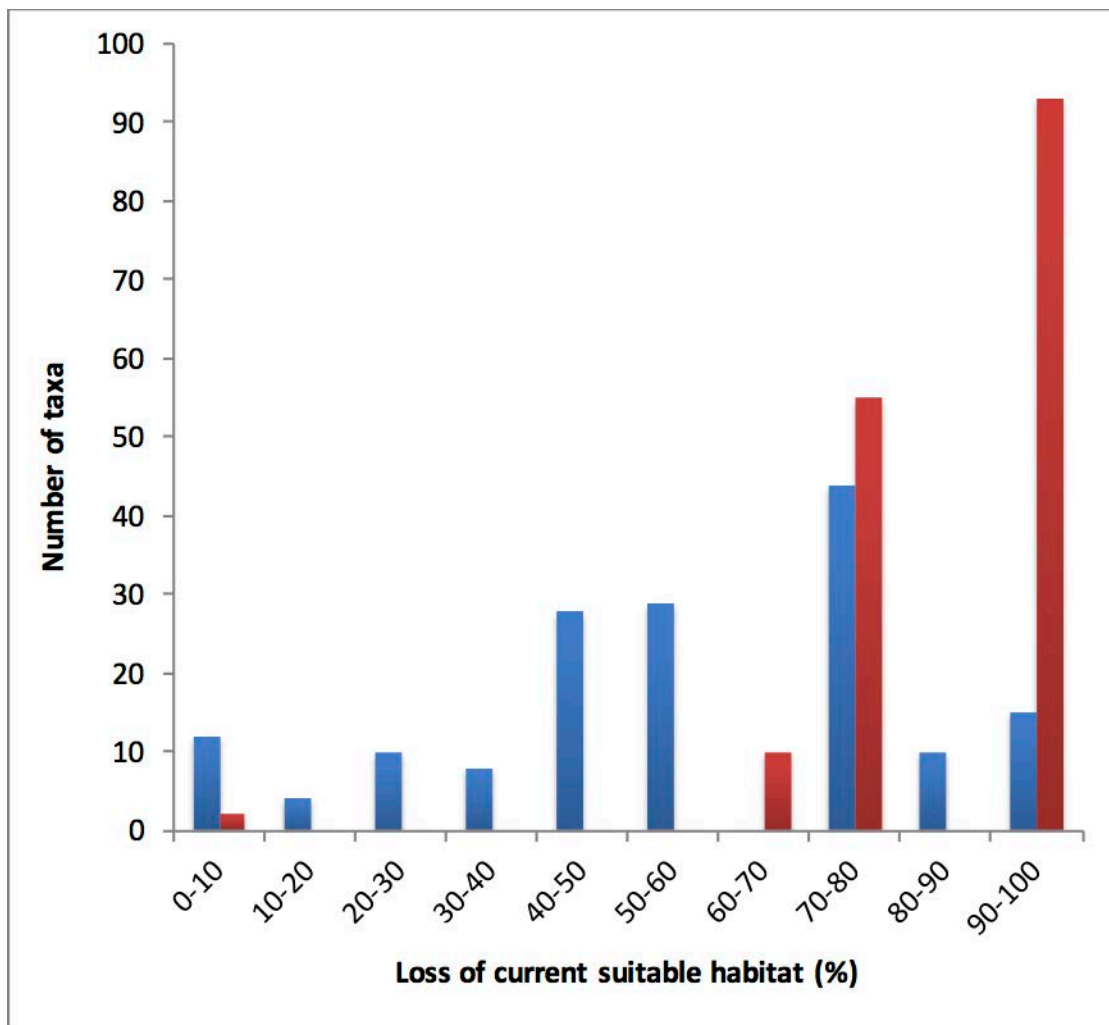
SUPPLEMENTARY INFORMATION

Table S1 Predicted land area changes for the recognised sections of the genus *Conophytum* under climate change scenarios A1B and A2. See Text / Table for abbreviations.

	AIB		A2	
Section	Positive change (%)	Negative change (%)	Positive change (%)	Negative change (%)
BAR	55.31	27.74	47.54	99.99
BAT	383.43	55.84	290.87	100.00
BIL	58.58	51.25	26.61	98.11
CAT	42.19	20.68	74.55	94.94
CHE	52.58	80.51	183.57	76.88
CON	1.81	94.59	0.79	99.03
COS	95.47	55.07	512.15	2.74
CYL	3.10	5.07	68.57	99.95
HER	133.51	38.33	298.65	72.73
MIN	29.99	78.40	41.33	77.53
OPH	31.16	50.39	72.88	68.02
PEL	1.64	56.86	73.79	100.00
SAX	7.03	72.44	0.06	100.00
SUB	123.45	1.13	263.76	70.70
VER	593.33	11.30	746.36	91.63
WET	31.05	45.26	15.52	99.26

Table S2. List of species in the genus *Conophytum* as recognised by Hammer and Young (2015). Locality data for all the 159 taxa listed here was u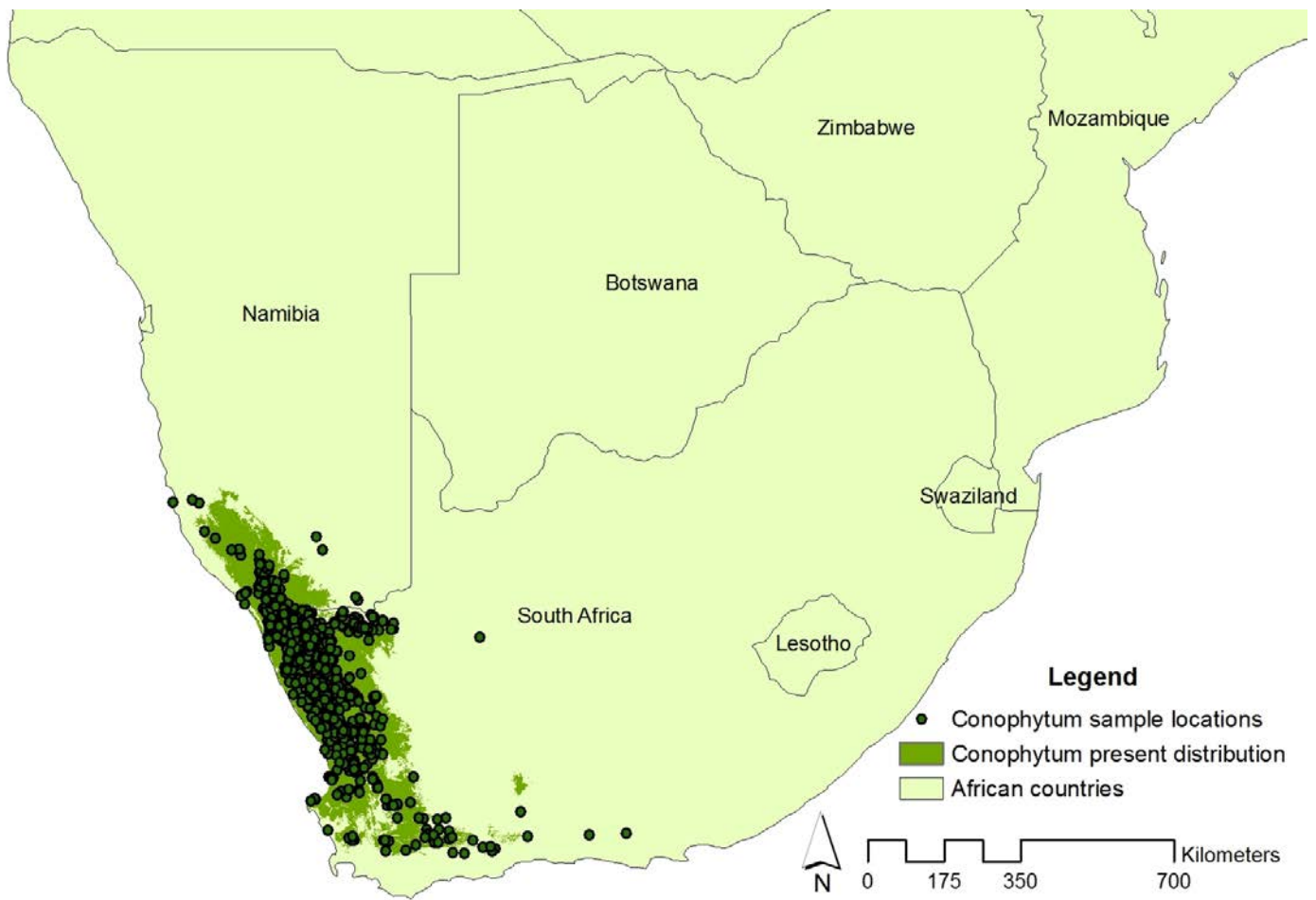sed in the climate change modelling. *C. semivestitum* and *C. herreanthus* ssp. *herreanthus* are both lost in habitat and therefore excluded from the study as were natural hybrids and any collections of uncertain taxonomy. Sections: BAR Barbata; BAT Batrachia; BIL Bilobum; CAT Cataphracta; CHE Cheshire-Feles; CON Conophytum; COS Costata; CYL Cylindrata; HER Herreanthus; MIN Minuscula; OPH Ophthalmophyllum; PEL Pellucida; SAX Saxetana; SUB Subfenestrata; VER Verrucosa; WET Wettsteinia (see Hammer, 2002).

SPECIES	SUBSPECIES	SECTION
C. achabense		CHE
C. acutum		CHE
C. albiflorum		MIN
C. angelicae	subsp. *angelicae*	COS
C. angelicae	subsp. *tetragonum*	COS
C. antonii		MIN
C. armianum		BAT
C. arturolfago		PEL
C. auriflorum	subsp. *auriflorum*	MIN
C. auriflorum	subsp. *turbiniforme*	MIN
C. bachelorum		WET
C. bicarinatum		MIN
C. bilobum	subsp. *altum*	BIL
C. bilobum	subsp. *bilobum*	BIL
C. bilobum	subsp. *claviferens*	BIL
C. bilobum	subsp. *gracilistylum*	BIL
C. blandum		HER
C. bolusiae	subsp. *bolusiae*	WET
C. bolusiae	subsp. *primavernum*	WET
C. breve		CAT
C. brunneum		MIN
C. bruynsii		MIN
C. burgeri		CHE
C. buysianum	subsp. *buysianum*	CYL
C. buysianum	subsp. *politum*	CYL
C. calculus	subsp. *calculus*	CAT
C. calculus	subsp. *vanzylii*	CAT
C. caroli		OPH
C. carpianum		SAX
C. chauviniae		BIL

C. chrisocruxum		WET
C. chrisolum		WET
C. comptonii		CON
C. concavum		SUB
C. concordans		OPH
C. cubicum		MIN
C. cylindratum		CYL
C. danielii		HER
C. depressum	subsp. *depressum*	BAR
C. depressum	subsp. *perdurans*	BAR
C. devium	subsp. *devium*	OPH
C. devium	subsp. *stiriiferum*	OPH
C. ectypum	subsp. *brownii*	MIN
C. ectypum	subsp. *cruciatum*	MIN
C. ectypum	subsp. *ectypum*	MIN
C. ectypum	subsp. *ignavum*	MIN
C. ectypum	subsp. *sulcatum*	MIN
C. ernstii	subsp. *cerebellum*	WET
C. ernstii	subsp. *ernstii*	WET
C. ficiforme		CON
C. flavum	subsp. *flavum*	WET
C. flavum	subsp. *novicium*	WET
C. francoiseae		WET
C. fraternum		WET
C. friedrichiae		OPH
C. frutescens		BIL
C. fulleri		MIN
C. globosum		WET
C. halenbergense		SAX
C. hammeri		CHE
C. hanae		MIN
C. hermarium		VER
C. herreanthus	subsp. *herreanthus*	HER
C. herreanthus	subsp. *rex*	HER
C. hians		SAX
C. hyracis		MIN
C. irmae		MIN
C. joubertii		CON
C. jucundum	subsp. *fragile*	WET
C. jucundum	subsp. *jucundum*	WET
C. jucundum	subsp. *marlothii*	WET
C. jucundum	subsp. *ruschii*	WET
C. khamiesbergense		CYL
C. klinghardtense	subsp. *baradii*	SAX
C. klinghardtense	subsp. *klinghardtense*	SAX
C. limpidum		OPH

C. lithopsoides	subsp. *boreale*	PEL
C. lithopsoides	subsp. *koubergense*	PEL
C. lithopsoides	subsp. *lithopsoides*	PEL
C. loeschianum		SAX
C. longibracteatum		MIN
C. longum		OPH
C. luckhoffii		MIN
C. lydiae		OPH
C. marginatum	subsp. *haramoepense*	HER
C. marginatum	subsp. *littlewoodii*	HER
C. marginatum	subsp. *marginatum*	HER
C. maughanii	subsp. *armeniacum*	CHE
C. maughanii	subsp. *latum*	CHE
C. maughanii	subsp. *maughanii*	CHE
C. meyeri		BIL
C. minimum		CON
C. minusculum	subsp. *aestiflorens*	MIN
C. minusculum	subsp. *leipoldtii*	MIN
C. minusculum	subsp. *minusculum*	MIN
C. minutum		WET
C. mirabile		MIN
C. obcordellum	subsp. *obcordellum*	CON
C. obcordellum	subsp. *rolfii*	CON
C. obcordellum	subsp. *stenandrum*	CON
C. obscurum	subsp. *barbatum*	WET
C. obscurum	subsp. *obscurum*	WET
C. obscurum	subsp. *sponsaliorum*	WET
C. obscurum	subsp. *vitreopapillum*	WET
C. pageae		CAT
C. pellucidum	subsp. *cupreatum*	PEL
C. pellucidum	subsp. *pellucidum*	PEL
C. pellucidum	subsp. *saueri*	PEL
C. phoenicium		CHE
C. piluliforme	subsp. *edwardii*	CON
C. piluliforme	subsp. *piluliforme*	CON
C. pium		MIN
C. praesectum		OPH
C. pubescens		OPH
C. pubicalyx		BAR
C. quaesitum	subsp. *densipunctum*	SAX
C. quaesitum	subsp. *quaesitum*	SAX
C. ratum		CHE
C. reconditum		CYL
C. regale		HER
C. ricardianum	subsp. *ricardianum*	WET
C. roodiae	subsp. *corrugatum*	CYL

C. roodiae	subsp. *roodiae*	CYL
C. roodiae	subsp. *sanguineum*	CYL
C. rugosum		CYL
C. saxetanum		SAX
C. schlechteri		WET
C. smaleorum		WET
C. smorenskaduense		VER
C. stephanii	subsp. *helmutii*	BAR
C. stephanii	subsp. *stephanii*	BAR
C. stevens-jonesianum		CAT
C. subfenestratum		SUB
C. subterraneum		CHE
C. swanepoelianum	subsp. *proliferans*	MIN
C. swanepoelianum	subsp. *rubrolineatum*	MIN
C. swanepoelianum	subsp. *swanepoelianum*	MIN
C. tantillum	subsp. *amicorum*	MIN
C. tantillum	subsp. *eenkokerense*	MIN
C. tantillum	subsp. *heleniae*	MIN
C. tantillum	subsp. *inexpectatum*	MIN
C. tantillum	subsp. *lindenianum*	MIN
C. tantillum	subsp. *tantillum*	MIN
C. taylorianum	subsp. *ernianum*	WET
C. taylorianum	subsp. *rosynense*	WET
C. taylorianum	subsp. *taylorianum*	WET
C. truncatum	subsp. *truncatum*	CON
C. truncatum	subsp. *viridicatum*	CON
C. turrigerum		MIN
C. uviforme	subsp. *decoratum*	CON
C. uviforme	subsp. *rauhii*	CON
C. uviforme	subsp. *subincanum*	CON
C. uviforme	subsp. *uviforme*	CON
C. vanheerdei		VER
C. velutinum	subsp. *polyandrum*	BIL
C. velutinum	subsp. *velutinum*	BIL
C. verrucosum		VER
C. violaciflorum		MIN
C. wettsteinii		WET
C. youngii		CYL

Legend

- Conophytum sample locations
- Conophytum present distribution
- African countries

Kilometers

| 0 | 175 | 350 | 700 |

N

Table S4 Contribution of variables for the present distribution of *Conophytum* Sections. Abbreviations: BAR Barbata; BAT Batrachia; BIL Bilobum; CAT Cataphracta; CHE Cheshire-Feles; CON Conophytum; COS Costata; CYL Cylindrata; HER Herreanthus; MIN Minuscula; OPH Ophthalmophyllum; PEL Pellucida; SAX Saxetana; SUB Subfenestrata; VER Verrucosa; WET Wettsteinia (see Hammer, 2002). T_{max} maximum temperature; T_{min} minimum temperature; T_{av} average temperature; P_{av} average rainfall.

VARIABLE	BAR	BAT	BIL	CAT	CHE	CON	COS	CYL	HER	MIN	OPH	PEL	SAX	SUB	VER	WET
Altitude	6.6185	1	0.3327	1.0388	4.4519	6.8379	5.1619	3.0104	13.9571	2.1215	11.9062	7.0852	0.4262	5.8784	19.5937	0.0203
Q1 T_{max}	0.0816	0.635	0.4526	1.8046	2.2861	4.4176	0.1137	0.4215	3.9857	0.7157	5.733	0.2381	6.8026	3.3825	7.2639	3.984
Q1 T_{min}	0	0	0.0012	0.0841	1.6157	1.9308	0	0.2241	3.8253	0.0158	0.5144	0.1295	0	0	0.336	0.174
Q1 P_{av}	29.171	47.0995	47.9971	37.9045	1.7774	19.8368	0.2117	0.8229	0.2511	24.3119	0.7942	16.6466	44.4089	44.8801	14.6578	55.7121
Q1 T_{av}	0	0	2.9185	0.1029	0.0308	0.2328	5.9636	0	0.0382	0.0467	0.0334	0	0.1052	0	0.7431	0.3443
Geology1	20.2934	17.3311	7.8256	29.491	42.9386	1.6521	40.4549	63.0088	54.6992	3.799	38.7484	47.6936	11.7368	10.819	46.6766	6.8834
Q2 T_{max}	2.0612	0	1.2705	0.2859	0.3147	0.4588	0.0666	0	0.0586	4.9733	0.0311	0.0442	0	0	0	0.0654
Q2 T_{min}	0.0457	0	0.4934	0.7646	7.0381	0.6145	0.8248	0.0332	0.9129	0.2436	1.1297	0.139	0.0473	4.1181	5.1898	0.1108
Q2 P_{av}	0.0502	0.301	6.1322	2.025	8.099	6.0773	7.0504	0.2983	0.1214	1.305	10.4734	0.0268	16.1713	3.7533	0	13.9128
Q2 T_{av}	0	0	0.0039	0.1755	0.0877	0.4793	0	0.1308	0	0.154	0.0112	0.0016	0	0	0	0
Geology2	12.8076	0.4653	2.1824	2.9662	1.4033	0.1268	15.0572	0	6.5485	25.4172	0.5325	0.7175	1.4932	0.1162	0	0.0465
Q3 T_{max}	0.0557	0	0.0433	1.0136	0.9736	0.2132	0	0	0.0613	8.2232	0.9662	0.0199	0.2119	0	0	0.0835
Q3 T_{min}	0.3915	12.2113	2.6293	4.1786	1.158	0.431	0	0.0164	0.2969	3.6665	14.5586	0.1543	0.2919	0	0	0.9547
Q3 P_{av}	24.7613	0.932	15.1277	16.1056	27.2111	49.4262	22.6823	31.7284	13.8596	12.7844	14.4477	25.5238	2.1197	26.1922	5.5344	14.1914
Q3 T_{av}	0	0	0.6716	0.2689	0.1288	0.4062	0	0	0	3.5007	0	0	0	0.588	0	0.034
Terrain	0.0029	8.4315	1.4723	0	0	5.9583	0.6942	0	0	3.74	0	0	7.0351	0	0	1.5032
Q4 T_{max}	0	0.0501	4.8427	0.0355	0.0106	0.0452	0	0	0	0.4684	0	0.0549	0	0	0	0.4269
Q4 T_{min}	0	0	0.0493	0.148	0.3272	0.071	1.1723	0.0144	0.0982	1.3121	0.0941	1.0573	0	0	0	1.0011
Q4 P_{av}	3.6593	11.543	5.4734	1.568	0.1475	0.7688	0	0.2909	1.2861	3.1885	0.0258	0.4193	9.1497	0.2721	0.0047	0.1567
Q4 T_{av}	0	0	0.0804	0.0388	0	0.0153	0.5465	0	0	0.0124	0	0.0486	0	0	0	0.3948