To converge or not to converge in environmental space: testing for similar environments between analogous succulent plants of North America and Africa

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• Background and Aims Convergent evolution is invoked to explain similarity between unrelated organisms in similar environments, but most evaluations of convergence analyse similarity of organismal attributes rather than of the environment. This study focuses on the globular succulent plants of the Americas, the cacti, and their counterparts in Africa in the ice-plant, spurge and milkweed families. Though often held up as paragons of convergent morphological evolution, the environmental similarity of these plants has remained largely unexamined from a quantitative perspective.

• Methods Five hotspots (centres of high species diversity of globular succulents) were selected, two in Mexico and three in South Africa. Their environments were compared using niche modelling tools, randomization tests of niche similarity and multivariate analyses to test for environmental similarity.

• Key Results Although the sites selected have ‘similar’ but unrelated life forms, almost all our results highlighted more climate differences than similarities between the hotspots. Interpretation of niches within and between continents, a niche equivalence test, and MANOVA results showed significant differences. In contrast, a niche similarity test showed that the comparisons of Cuatrociénegas–Richtersveld, Huizache–Knersvlakte and Huizache–Richtersveld were similar.

• Conclusions Differences in rainfall and temperature regimes and the potential effect of edaphic factors may be involved in the differences between the hotspots. In addition, differences in structure, morphology and physiology of the globular succulents may coincide with some of the climatic dissimilarities; i.e. given convergence as the evolution of similar morphologies under similar conditions, then it may be that differing environments diagnose inconspicuous morphological differences. Moreover, although fine-scale differences between sites were found, a coarser perspective shows that these sites are clearly similar as drylands with relatively moderate drought and mild temperatures, illustrating how all studies of convergence must address the issue of how similar two entities must be before they are considered convergent.

Key words: Adaptation, convergent evolution, environmental similarity, niche modelling, succulent plants.

INTRODUCTION

Convergent evolution is a central topic in comparative biology because it is often taken as evidence of adaptation by natural selection (Harvey and Pagel, 1991; Larson and Losos, 1996). Similar attributes in unrelated groups reflect adaptive responses to similar environmental pressures, even though the initial ancestral states were different (Orians and Paine, 1983; Stearns and Hoekstra, 2000; Revell et al., 2007). Convergent evolution has been documented in many cases, including classic examples involving morphological, ecological and behavioral similarities between placental and marsupial ‘wolves’ (Werdelin, 1986; Wroe et al., 2007), the similar wing shape and size of bats and birds (Norberg, 1981), or the morphological similarity between the cacti of the Americas and spurge and milkweeds of Africa (Peet, 1978; Bennici, 2003). Because the central prediction of convergence is similar organismal structure and function in similar environmental contexts, it is crucial to evaluate the similarity of the environment just as carefully as organismal similarity.

Most convergence studies have focused on biological attributes as opposed to environmental ones, including morphology (Losos, 1992; Stayton, 2005), community structure (Parsons and Moldenke, 1975; Esler and Rundel, 1999; Melville et al., 2005), physiology (Reich et al., 1997; Meinerz, 2003) and species diversity (Schluter and Ricklefs, 1993). All these studies have provided useful information to understand convergence (Codon and Mooney, 1978; Esler and Rundel, 1999), but because they included only qualitative descriptions of the environment or coarse climatic measurements, they have left untested the crucial assumption of similar environmental pressures.

Newly available climate data allow examination of the environmental aspect of convergence predictions. Convergence
in climatic conditions can be interpreted as overlap in environmental space; in contrast, divergence can be interpreted as different areas in environmental space. These spaces can be estimated from layers of climate variables, reflecting how similar the entities are in their environmental requirements. Environmental information now available (Hijmans et al., 2005) and the tools of geographic information systems (GIS) and species distribution modelling (SDM) make it possible to quantify environmental space for virtually any point on Earth, and to quantify and evaluate their similarities and differences at fine resolution in numerous variables (Kozak et al., 2008; Warren et al., 2008). These tools are able not only to compare climatic factors quantitatively, but they can also help identify environmental factors potentially driving the evolution of a given morphological trait (Kozak et al., 2008), including in a convergent fashion. By finding that dissimilar selective pressures lead to similar morphologies may help reject a hypothesis of convergence (Peet, 1978; Melville et al., 2005).

To test the hypothesis of convergence in environmental requirements quantitatively, we have selected the classic example of apparent convergent evolution between the succulent plants of the American arid regions, the cacti, and their distantly related African analogues, the milkweeds (Apocynaceae), spurge (Euphorbiaceae) and ice-plants (Aizoaceae). This case has illustrated convergent evolution in countless publications for over 100 years (a small selection of examples is presented in Table 1), but quantitative comparisons have been rare and based mainly on morphology rather than environment (Orians and Solbrig, 1977; Felger and Henrickson, 1997; Trager, 1985; Mauseth, 2004). Selection favouring low surface : volume ratios is universally invoked as a potential driving factor in the evolution of succulents (Warming, 1909; Gibson and Nobel, 1986; Mauseth, 2000; Melville et al., 2005).

Therefore, to test the hypothesis of climatic convergence, we selected the globular succulent plants that are found in Cactaceae, Euphorbiaceae and Apocynaceae, which are derived from stems, and those in Aizoaceae, which are derived from leaves (Fig. 1). From different ancestral states unrelated lineages have arrived at similarly globular morphologies under putatively similar selective environments. We selected succulents in general and globular ones in particular as a study system because of a remarkable unanimity in the literature regarding the selective factors behind their evolution. We are aware of no factor other than selection favouring low surface : volume ratios ever having been proposed to explain the spherical bodies of the cacti, ice-plants, spurge and milkweeds, despite their differing anatomical constructions. As a result, the cacti and Old World globular succulents represent an ideal model to test the assumption of environmental similarity implicit in the unchallenged assumption that the globular succulents represent similar responses to similar selection pressures.

We present the first quantitative attempt to evaluate the pervasive assumption of convergence among globular succulent plants from a bioclimatic perspective. We selected the succulent communities of Cuatrociénegas and El Huizache in the Mexican Chihuahuan Desert, and the Knysnvletke, the Little Karoo and the Richtersveld in the Succulent Karoo, South Africa, because these areas have been singled out as the global hotspots of globular succulent plant diversity (Olson and Dinerstein, 1998; Cowling and Hilton-Taylor, 1999; Hernández et al., 2001; Wyk and Smith, 2001; see Fig. 2). In the terms of the methods used here, our prediction is that areas with high species diversity of putatively similar globular succulents should overlap in environmental space. If similar sets of environmental pressures favour similar growth forms, then the areas of highest diversity of similar globular succulents should diagnose areas of potential climatic similarity. The sites we compared in Mexico and South Africa together support the highest diversity known of globular succulents (Fig. 1). In addition to species diversity, the hotspots are also areas of some of the greatest globular succulent abundance. Although some globular taxa are soil specific (Schmiedel and Jürgens, 1999, 2004), to our knowledge, all hypotheses that have ever been presented to explain the similarity in forms between the succulents of different families on different continents involve the assumption of similar environmental conditions (Table 1; Cowling et al., 1986; Esler et al., 1999; Hernández et al., 2001; Schmiedel et al., 2010).

Through our analyses we show how the use of GIS and SDM tools is ideal for detailed evaluation of environmental similarity between globular succulent hotspots in Mexico and southern Africa and discuss reasons for the overlap and lack thereof in our climate data. We conclude with points highlighted by our study that are of relevance to studies of convergence in general.

MATERIALS AND METHODS

Study sites

To test the often-repeated assumption of environmental similarity between the sites of globular succulent occurrence (Table 1), we selected the main areas perennially singled out as the global hotspots of succulent diversity. We selected these hotspots given that globular succulent species diversity is distributed highly unevenly across the world (Hernández et al., 2001; Wyk and Smith, 2001; Hernández and Gómez-Hinojosa, 2011), and it seems reasonable to expect that the areas of highest species diversity and abundance of globular succulents should coincide with areas of maximal environmental similarity. Two of these hotspots were in the Chihuahuan Desert, Mexico (MacMahon and Wagner, 1986; Hernández and Bárquen, 1995; Arriaga et al., 2000; Hernández et al., 2001), and three were in the Succulent Karoo of South Africa (Olson and Dinerstein, 1998; Cowling and Hilton-Taylor, 1999; Wyk and Smith, 2001; Fig. 2; Supplementary Data 1). In Mexico, we selected the two extraordinarily cactus-rich regions known as Cuatrociénegas and El Huizache, both of which in sheer species number far exceed any other similar-sized tracts of the Americas (Desmet and Cowling, 1999; Dinerstein et al., 2000; Hernández et al., 2001). Our delimitation of these areas follows Arriaga et al. (2000) and Hernández et al. (2001). In South Africa, we
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<td>Warming</td>
<td>1909</td>
<td>See also Glass and Foster, 1975</td>
<td>The most common and extreme types are Cactaceae in America, Stapelia in South Africa, and species of Euphorbia which occur mainly in Africa. In the various genera there occur a series of shapes whose efficiency has been demonstrated. Frequent among such shapes are those like the sphere, prism, or cylinder that combine smallness of surface with largeness of volume. Cactus stems are succulent. However, some plants of other families have succulent stems or leaves, and some even have the appearance of cacti. For example, the African succulent spurge (Euphorbia) seem almost identical with some cacti. In the deserts and semideserts of the American continent, the members of the Cactaceae are the outstanding examples of adaptation to the environment. Here we find shrubby species, columnar plants and globular types. Wherever similar conditions prevail in the Old World, it will be noticed that plants from many different families have been compelled to make these modifications. The growth forms of cacti, indigenous exclusively to the New World, under similar climatic conditions are duplicated as convergents in plant groups of the Old World. This is true not only of the common columnar form but also of the considerably rarer extreme-spherical forms.</td>
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<td>Benson</td>
<td>1969</td>
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<td>Jacobsen</td>
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selected the globular succulent hotspots known as the Richtersveld, Knersvlakte and Little Karoo (Cowling et al., 1998; Wyk and Smith, 2001; Schmiedel and Jürgens, 2004) as delimited by the Succulent Karoo Ecosystem Program (Driver et al., 2003). Although the Chihuahuan and Karoo deserts have contrasting rainfall periods, with summer versus winter rainfall, respectively (Hernández and Bárdenas, 1995; Desmet and Cowling, 1999; Wyk and Smith, 2001), their strikingly similar globular succulents (Fig. 1) and high globular species diversity has prompted frequent comparisons with American succulents and claims of convergence (Cowling, 1986; von Willert et al., 1992; Cody, 1991; von Willert et al., 1992; Cowling and Hilton-Taylor, 1999; Hernández et al., 2001; Schmiedel et al., 2010), and because the fine resolution of these layers allowed a detailed assessment of the environmental characteristics of the globular hotspots.

Environmental variables, species occurrence localities, and species selection

To characterize the environmental spaces of the globular centres, we used 19 bioclimatic variables (Supplementary Data 2) from WorldClim (Hijmans et al., 2005), a global set of climate layers generated by interpolation of climate data from weather stations. The raster grids of the variables employed here had a spatial resolution of 30' (approx. 1 km² resolution). We selected this environmental information because, in the literature, the geographic distribution, growth forms, reproduction and establishment of succulent plants are mainly attributed to climatic conditions to an overwhelming degree as compared with other factors such as soils or biological interactions (Cowling, 1986; Nobel et al., 1986; Cody, 1991; von Willert et al., 1992; Cowling and Hilton-Taylor, 1999; Hernández et al., 2001; Schmiedel et al., 2010), and because the fine resolution of these layers allowed a detailed assessment of the environmental characteristics of the globular hotspots.

To extract climatic information, we obtained occurrence localities from the BOL, HTN, MEXU and NGB herbaria (Holmgren et al., 1990) for each globular succulent species in each hotspot, and from fieldwork in the Knersvlakte and Richtersveld, South Africa, and El Huizache, Mexico. We also consulted the Pretoria Computerized Information Systems database of the South African National Biodiversity
Institute and the Database of Cactus Collections from North and Central America (Hernández and Gómez-Hinostrosa, 2011). We compiled a total of 498 locality records for 89 South African species, and 821 records for 57 Mexican taxa (Supplementary Data 3). To reduce the effects of sampling bias, we removed the localities with similar co-ordinates to obtain unique records, and we ensured that the localities fell mainly in distinct grids of the bioclimatic layers.

We selected the globular succulent species based on the examples illustrated in numerous publications (Table 1). Globular succulents are found in several families, but mainly in Cactaceae, Euphorbiaceae, Apocynaceae and Aizoaceae. Regardless of the construction of the stem or leaf, selection in dry habitats favouring minimal surface area is always invoked in explaining why these species have their spherical shape (Glass and Foster, 1975; Gibson and Nobel, 1986; Mauseth, 2000; McGhee, 2011). These globular groups allowed us to test the expectation that similar globular morphologies should be found in similar selective environments. We selected the species with vegetative structures consisting of succulent organs, which are individually described as globular, semiglobular, spherical or subspherical, those with similarly wide and tall dimensions, or those wider than tall for extended periods of their life cycle. We identified species as meeting this definition based on taxonomic descriptions, specimen label information and field observations.

Modelling algorithm

A hypothesis of convergent evolution assumes that similar environmental pressures should result in similar organismal responses. We built our analyses around this assumption, which implies that the globular succulent hotspots around the world should reflect similar climate conditions. Environmental niche models are typically used to model the potential distribution of a single species, but for our question the appropriate sampling scheme was to use occurrence data for all globular species within each hotspot as the basis for our models.

We built these models using the program MaxEnt v. 3.2.1. (Phillips et al., 2006), which models based on presence records only and samples ‘pseudo-absences’ to calculate the model performance measures, making it appropriate for our study, which included only presence data. We used 70% of
records as training data and 30 % for testing the model. We constructed the models using the 19 sets of bioclimatic layers, and we also applied a principal component analysis (PCA) to the set of layers in ArcGIS 9.3 (ESRI, 2006). Although the models with the complete dataset were very similar to those generated using the PCA layers, we present results based only on the first three PCA-reduced variables (Table 2) because these reduced layers helped to compensate for possible overparameterization of models caused by multicollinearity. Moreover, we performed the statistical comparisons between sites with only the reduced dataset due to the extensive computational time required in the performance of the tests (see next section). The models generated by the complete dataset are available from the first author. We used default settings for all analyses to measure the degree to which the models differed from random using the AUC, the area under the receiver operating characteristic curve. The AUC scores are interpreted as reflecting the ability of the model to distinguish presence data from background data (Phillips et al., 2006).

### Tests of environmental similarity

To examine the assumption of environmental similarity between the globular hotspots of Mexico and southern Africa, we first compared the maps resulting from the MaxEnt model outputs from one globular centre against the other hotspots between continents. These comparisons gave us a starting point to evaluate the potential similarity or dissimilarity between the globular succulent centres.

Our following step was to quantify the environmental overlap between sites using the niche equivalence and similarity tests of Warren et al. (2008), expressing the results of both tests via Shoener's D score (Schoener, 1968; Warren et al., 2008), in which similarity is scaled from 0 (no overlap) to 1 (complete overlap). We used ENMTools v.1.3 (Warren et al., 2008, 2010) to implement both tests. Calculating D requires two key items of information, the modelled distribution area, i.e. preferred climate conditions of globular succulents of one area (say, Cuatrociénegas) and the model distribution of another area (e.g. the Knersvlakte). These models are expressed as probabilities, understood as the probability of finding suitable conditions for globular succulents at any given pixel within the area being examined, given how suitable or not the climate at the given pixel is. For a given site (e.g. Cuatrociénegas), we can therefore compare the probability of finding globular succulents for each pixel given the ‘native’ model based on the distribution of cacti at Cuatrociénegas \( p_{x,i} \) and compare the probability of finding globular succulents in those same pixels but using the ‘foreign’ model generated from the succulents occurring at another site, such as the Knersvlakte \( p_{y,i} \). As implemented by ENMTools, \( p_{x,i} \) and \( p_{y,i} \) are divided by the total number of pixels so that over all \( p_{x,i} \) and \( p_{y,i} \) both sum to unity. The absolute value of the differences between \( p_{x,i} \) and \( p_{y,i} \) for a given pixel thus gives an index of how similar the climate is in that pixel with respect to globular succulents and, by summing all of them, we obtain a rough comparison of climate similarity between two sites.

For the equivalence test, we generated two distribution models based on randomizing a pooled occurrence dataset from a pair of sites. This process generates two datasets of the same size as the original ones. For each dataset, ENMTools uses MaxEnt to project the model distribution to each globular centre and, subsequently, it calculates the D statistic based on the predicted suitability scores for each pixel. We repeated this process 100 times to create a null distribution against which to compare the observed D scores. The hypothesis of equivalence was rejected when the observed values for D were significantly lower than the values expected from the critical values of the null distribution datasets (0.01) and was not when the observed values fell within those expected from the null distribution datasets. The preceding test is appealing because it is simple and similar to other comparison tests (e.g. the incongruence length difference test of molecular phylogenetics; Farris et al., 1995) and therefore provides a familiar metric by which to compare datasets. However, unless the exact points where the organisms were found in both sites are very similar climatically, the test will tend to reject the notion that the sites are identical.

The so-called similarity test is somewhat less stringent. The similarity test compares the observed values of D with those calculated from the niche model generated from the occurrence data at one hotspot with the model generated from points selected at random from within the other hotspot. In this way, we can see whether the climate of one area is statistically indistinguishable with that obtaining in the general area (as opposed to that in the exact points of occurrence) of the other hotspot. There are many possible ways of defining ‘similar’, and, like the previous one, this test offers a similarity index that is readily understood and is of familiar structure. We sampled at random from within the distribution of the ‘other’ hotspot by constructing a mask layer based on the minimum training presence value from the model predicting areas of each centre (Table 3), and we delimited the predictions using the biogeographical limits for each hotspot. We repeated this entire procedure 100 times for each site and in two directions, from site A to site B and vice versa. The expected null distribution of D scores was compared with those from the actual dataset in a two-tailed test. The hypothesis of similarity was rejected when the observed values for D were significantly lower than the critical values of the null distribution (0.01) and was not when the observed values were higher than expected from the null distribution datasets.

We also tested for significant differences between the areas using a multivariate analysis of variance (MANOVA) to compare the estimates of the mean for each environmental variable in each globular centre. Instead of using information

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<th>Table 2. The first three axes of the PCA of bioclimatic variables resulting from ArcGIS analysis</th>
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<td>PCA1: 10 = mean temperature of warmest quarter, 17 = precipitation of driest quarter</td>
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<td>PCA2: 4 = temperature seasonality, 5 = max temperature of warmest month, 8 = mean temperature of wettest quarter</td>
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<tr>
<td>PCA3: 3 = isothermality, 9 = mean temperature of driest quarter, 13 = precipitation of wettest month, 14 = precipitation of driest month, 18 = precipitation of warmest quarter</td>
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In turn, we projected the South African models to Mexico (Fig. 4). Here again, model projections from the Richtersveld and Knersvlakte failed to predict the Mexican hotspots, falling instead in small areas of the southern part of the Chihuahuan Desert and Balsas Depression respectively (Fig. 4A–D). The Little Karoo was the only comparison congruent with our main hypothesis of similarity, predicting the southern portion of the Chihuahuan and El Huizache region with striking similarity (Fig. 4E, F).

**Niche equivalence test**

The so-called equivalence test (Warren et al., 2008) evaluates the hypothesis that there are no significant environmental differences between the entities compared based on the climate data obtained from the exact points of occurrence of the species studied within each hotspot. The test rejected the null hypothesis of equivalence among the compared sites (Table 5).

**Niche similarity test**

The similarity test evaluates whether the model from one area differs significantly from that generated based on a sampling of random points from another hotspot. The sites compared are considered similar only if the D-values are higher than the critical values of the null distributions (Warren et al., 2008, 2010). The paired comparisons that were considered similar were Cuatrociénegas–Richtersveld, Huizache–Knersvlakte and Huizache–Richtersveld (Table 6).

**MANOVA**

We used a nonparametric MANOVA, Kruskal–Wallis tests and the Behrens–Fisher *post hoc* test as a complement to our modelling approach to evaluate the similarity between globular centres (Table 7). We applied these analyses on the first three PCA axes, which explained the 96% of the variance (Table 4). The MANOVA results showed that at least one of the five sites differed in their mean environmental properties ($F = 410.24$, d.f. 4, $P = 0.001$), and the Behrens–Fisher *post hoc* tests were significant for all the comparisons ($P = 0.001$), thus rejecting the hypothesis of environmental similarity between hotspots.

**Discussion**

Convergent evolution is thought to be driven by similar environmental conditions leading to similar selective pressures, for which there are similar evolutionary responses in unrelated lineages (Orians and Solbrig, 1977; Orians and Paine, 1983; Esler and Rundel, 1999; McGhee, 2011). In the case of the suggested convergence between succulent plants of the American and African drylands (Table 1), we would expect to find similar environmental conditions in the areas where globular plants are most diverse and abundant. Yet, despite their striking morphological similarity (Fig. 1) and their putatively similar environments, we found conspicuous differences in climate between the succulent hotspots of Mexico and South Africa. With some exceptions, our analyses based on
FIG. 3. PCA model building and projection for Cuatrociénegas and El Huizache, Mexico: (A) predictive model for the species of Cuatrociénegas; (B) model projection from Cuatrociénegas, Mexico to southern Africa; (C) predictive model for the species of El Huizache; (D) model projection from El Huizache to southern Africa. Shading indicates levels of model prediction, with scales as shown. Numbers and lines on the map of southern Africa denote (1) Richtersveld, (2) Knersvlakte and (3) Little Karoo.
Fig. 4. PCA model building and projection for the Richtersveld, Knersvlakte and Little Karoo, South Africa: (A) predictive model for the species of the Richtersveld; (B) model projection from the Richtersveld to Mexico; (C) predictive model for the species of the Knersvlakte; (D) model projection from the Knersvlakte to Mexico; (E) predictive model for the species of the Little Karoo; (F) model projection from the Little Karoo to Mexico. Shading indicates levels of model prediction, with scales as shown. Numbers on the map of Mexico denote (1) Cuatrociénegas (polygon) and (2) Huizache (square). Areas outlined on the map of southern Africa as is indicated in Fig. 3.
distribution models (Figs 3A–D and 4A–D), niche equivalence and similarity tests (Warren et al., 2008) (Tables 5 and 6) and multivariate analyses (Table 7) suggested that globular succulent centres on different continents are in different areas of environmental space.

These differences can be illustrated by inspecting maps of model projections between continents. When we projected the climate conditions of Cuatrociénegas to southern Africa, they mainly predicted the area of the Nama Karoo, adjacent to the Succulent Karoo (Fig. 3A, B). However, the Nama Karoo is dominated by shrubs and tall stem succulents and grasses with very few globular succulents in comparison with the Succulent Karoo and Cuatrociénegas (Wyk and Smith, 2001; Hartmann, 2004, 2006). Similarly, the model projections from the South African Knersvlakte and Richtersveld did not predict the Mexican hotspots (Fig. 4A–D). Thus, despite the gross morphological similarities between Mexican and South African succulents (Fig. 1), our climate maps suggest that they occur in areas with different climates.

The statistical yardsticks we used highlighted these differences. The hotspots had generally quite different climates based on the equivalence, similarity and MANOVA tests (Tables 5–7). The niche equivalence test essentially mixes the occurrence data from two hotspots. If the two original data-sets are made up of points falling in very similar climates, then the resulting projections will be similar to the originals. With this procedure, all possible pairs of intercontinental comparisons were significantly different from one another (Table 5) despite the apparent morphological similarity of their plant complements (Fig. 1). The similarity test involved comparing the observed climate of one hotspot with that found in another hotspot, as inferred from random points within it. Because it has the potential to include a greater environmental range within the other distribution, the similarity test can be considered less stringent regarding what is to be taken as similar. Accordingly, this test showed Cuatrociénegas to be similar to the Richtersveld, and El Huizache was more similar to the Richtersveld and to the Knersvlakte than we would expect given the null distribution generated (Table 6). The MANOVA results also suggested significant differences in all intercontinental comparisons (Table 7). While the succulent hotspots are no doubt similar in that they are drylands, they differ in major details of their rainfall and temperature regimes and points of similarity were fewer than the differences.

These differences among the tests inevitably raise the question of why, then, these plants look so similar, at least superficially, and why we did not find more climatic coincidence. One possibility is that the climatic variables employed do not include critical limiting factors (e.g. proximity to the ocean, water input in form of fog and dew, soil, biotic interactions, etc.) that may drive the evolution of convergent globular life forms. For example, when we projected the climate conditions of Cuatrociénegas to Africa, they fell mainly in the area of the Nama Karoo, which has tall rather than globular succulents and is adjacent to, rather than within, the globular-rich Succulent Karoo. This discrepancy in areas of prediction may be explained because both Cuatrociénegas and the Nama Karoo have summer rainfall and strong rain shadows (MacMahon and Wagner, 1986; Arriaga et al., 2000; Wyk and Smith, 2001; Fig. 3B). Another factor potentially involved in the differences between hotspots is the presence of azonal habitats such as quartz islands within the Succulent Karoo. Quartz islands are characterized by a dense layer of small quartz pebbles forming patches of variable sizes (Schmiedel and Jürgens, 1999, 2004). The environmental conditions in the quartz islands provide a selective regime abruptly distinct from the surroundings (Desmet and Cowling, 1999; Schmiedel and Jürgens, 1999). The soil affinities of cacti in Mexico are not well understood (McAuliffe, 1994; Bárcenas-Argüello et al., 2010). Some Mexican cacti are clearly soil specialists (e.g. Geohintonia and Aztekium), but for the most part the Mexican hotspots are on limestone-derived soils of wide occurrence and not edaphic islands (Hernández et al., 2001). Our results coincide with previous suggestions of differences in precipitation regime between the summer rainfall Chihuahuan Desert and the winter rainfall Succulent Karoo (Cowling et al., 1998; Desmet and Cowling, 1999; Esler and Rundel, 1999). The western coast of South Africa contrasts with the American inland deserts due to the reliability of its rainfall and its closeness to the Atlantic Ocean. This proximity mitigates the aridity of the Karoo, moderating its temperature and providing a constant supply of dew (Cowling et al.,
1998; Desmet, 2007). Thus, through its largely coincident results, our study offers the first quantitative comparison between the climates of the world’s main diversity centres of globular succulents and points to important differences among them.

A possible explanation for the climatic discrepancies we found is that the morphologies considered ‘similar’ in fact are differentiated either structurally or functionally in biologically important ways. While the globular groups we compared are often referred to as morphologically similar (Fig. 1 and Table 1), they are constructed in different ways (Hartmann, 2004; Mauseth, 2004). These differences could allow them to explore different sets of climatic conditions (Noble, 1982, 1989; von Willert et al., 1992). For example, the dominant group in the African hotspots is the ice-plant family (Cowling et al., 1994; Hartmann, 2004, 2006; Cowling et al., 1998), whose globular bodies are made up of leaves, whereas those of cacti are stems. Ice-plant bodies tend to be smaller than cacti, have shorter roots and short life spans, in contrast to the long-lived stems of cacti. Perhaps because of this rather frail construction, the succulent Aizoaceae have lower tolerance to drought and thermal stress than stem succulents like cacti or spurges (Noble, 1982; von Willert et al., 1992; Cowling et al., 1994; Jürgens et al., 1999). The apparently fragile construction of the globular Aizoaceae might represent an adaptation to the benign microclimate of the quartz soils (Desmet and Cowling, 1999; Schmiedel and Jürgens, 1999), to which some of them seem particularly restricted. In the case of stem succulents, their secondary growth, tough epidermal regions, deeper and woodyer roots and generally larger stature may give them more marked resistance to drought and heat (Gibson and Nobel, 1986). Thus, despite their overall similarity, in that they are both globular, the morphological features of cacti probably allow them to explore a wider area of environmental space as compared with the globular Aizoaceae. For example, the mostly globular genus Mammillaria is found across a vast range from the southwestern USA to northern South America, far larger than the area occupied by globular Aizoaceae. Accordingly, the model projections from cactus hotspots fell in areas drier or wetter than the Aizoaceae hotspots, such as the Nama Karoo or the southern coast of Africa, respectively. Physiologically, these groups also appear to be distinct. The Aizoaceae display significant flexibility of photosynthetic behaviour (Borland et al., 2011), while Cactaceae are obligate CAM plants. In addition, the plants classified as globular might differ when shape is studied quantitatively (Table 1 and Fig. 1). Some plants that are globular at younger developmental stages reach non-globular shapes with age, such Euphorbia obesa, perennially cited in comparisons with cacti (Glass and Foster, 1975; Trager, 1985; Gordon, 1997; McGhee, 2011). These differences in forms may translate into a lack of overlap in morphological space, implying that they may occupy different climatic conditions. Thus, the combination of structural, morphological and physiological differences could allow different groups of succulent plants to occupy distinct environments.

A final consideration, and one crucial for all studies of convergence, is the scale of analysis and what is understood by ‘similar’. Our interest was to make comparisons as fine as the available data and tools permit, and this approach pin-pointed abundant differences between areas where presumably convergent life forms occur. Coarser level comparisons almost certainly would show similarities rather than differences. Taking a global perspective, the drylands of southern Africa and the Americas are certainly more similar than the prairie, Mediterranean shrublands and tropical woods that surround the succulent hotspots on both continents. Succulent global plants can explore a wide variety of climatic conditions (Noble, 1982; Gibson and Nobel, 1986; von Willert et al.,
but the hotspots of globular plants seem to be drylands that have relatively predictable rainfall and moderate extremes of heat (von Willert et al., 1992; Hernández and Bárcenas, 1995; Hernández et al., 2001), as opposed to the markedly more severe Atacama, Namib or Sahara deserts. From a more global perspective, then, the globular hotspots are certainly similar in many regards.

Conclusions

Convergent evolution is the appearance of ‘similar’ morphologies under ‘similar’ selection regimes. However, there is no objective definition of ‘similar’ and any definition that we choose obeys the pragmatic considerations of a given study rather than some absolute standard of similarity. Different definitions will often yield differing results, as in the fine scale versus global comparisons discussed above. Such differences can even be found among our results. Whereas the niche equivalence test global comparisons discussed above. Such differences can even be found among our results. Whereas the niche equivalence test rejected their identical environment, according to the similarity test, the succulent centres of Cuatrociénegas–Richtersveld, Huizache–Richtersveld and Huizache–Knorsvlakte showed similar conditions. Our pragmatic use of ‘similarity’ was to compare climate models between continents with a series of well-known metrics to discover fine-scale differences or similarities. These fine-scale climatic differences can be used to guide further morphological studies of these plants. In particular, the qualitative impression of ‘similar shape’ so frequently invoked in examples of convergence bears re-examination, e.g. via techniques such as geometric morphometrics. Such an approach would allow quantification of shape similarity and allow testing of the hypothesis that species that are closer in shape space should also be closer in niche space.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Data 1: site descriptions. Data 2: list of 19 bioclimatic variables that were analysed. Data 3: species checklist of the different families of succulent plants used in the analyses.

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