



# Lineage-specific climatic niche drives the tempo of vicariance in the Rand Flora

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## ABSTRACT

**Aim** The disjunct distribution patterns of sister taxa can arise when previously continuous distribution ranges are fragmented by environmental changes such as major climatic events. Populations become isolated on either side of the newly established environmental barrier, and absence of gene flow promotes allopatric speciation, in a process that is known as ecological vicariance. If climate change altered the ancestral range gradually, such as along temporal temperature or moisture gradients, the age of divergence of disjunct species should be related to the lineage tolerance to climatic conditions. Here, we investigate this hypothesis using as a study model the African Rand Flora, a continental-scale floristic pattern that relates sister taxa distributed on either side of the Saharan Desert.

**Location** Africa, Macaronesia, Mediterranean Basin and the Middle East.

**Methods** We estimated the extant climatic tolerances of 14 Rand Flora lineages based on present occurrence data, and correlated the phylogenetic age of divergence between vicariant clades. We tested whether the tempo of the vicariance in the Rand Flora lineages was associated with the average values of their climatic niches in agreement with niche-driven divergence. We hindcasted species ranges using species distribution models combined with palaeoclimate simulations to infer the potential distribution of each lineage's ancestors.

**Results** We found a positive relationship between the lineage temperature niche and the age of the Rand Flora disjunction: lineages with subtropical affinities diverged first, whereas those with a higher tolerance to drier conditions (temperate or sub-xeric adaptations) exhibited younger disjunctions. The range reconstructions showed the existence of climatic corridors south of the Sahara in the wetter Late Miocene, which became interrupted during the mid-Pliocene warming event.

**Main conclusions** Our results suggest that climate change leading to the formation of the Sahara Desert drove Rand Flora lineages divergences along a temporal sequence that matched the climatic niche of species.

## Keywords

continental disjunctions, extinction, niche conservatism, Rand Flora, refuges, vicariance

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## INTRODUCTION

The concept of vicariance dates back to the origins of modern historical biogeography (Croizat, 1952; Brundin, 1967): vicariance arises when the ancestral range of a species

becomes divided by the appearance of a new biogeographical barrier, followed by allopatric speciation (Humphries & Parenti, 1999; Sanmartín, 2012). Although vicariance has often been associated with geological events, such as the formation of a mountain chain or an ocean basin between two tectonic

plates, this process refers to any environmental change that impacts a species geographical range. For example, a dramatic event of climate change might create new environmentally unsuitable area for a given species; individuals are unable to persist or disperse through these areas of unsuitable conditions, and the species distribution becomes fragmented (Wiens, 2004). The concept of ecological vicariance is strongly associated with the idea of niche conservatism, the tendency of species to retain their ancestral environmental preferences (Harvey & Pagel, 1991; Peterson *et al.*, 1999; Wiens & Graham, 2005; Wiens *et al.*, 2010; Crisp & Cook, 2012). In ecological vicariance, the rate of environmental change is faster than the species rate of adaptation, compelling the species to migrate or persist in residual suitable areas (Wiens, 2004). Vicariance is often associated with a general pattern of geographical fragmentation that is not unique to a single species but shared across unrelated lineages (Sanmartín, 2012). For ecological vicariance, this is the equivalent of an abrupt change in climate so rapid, intense and spatially widespread, that its effects are felt clade-wide across different lineages that present similar ecological affinities within the same geographical region.

Disjunct distribution patterns may result from the breaking of connectivity between previously continuous ranges. In comparison with transoceanic disjunctions (Wen, 1999; Xiang *et al.*, 2000; Sanmartín *et al.*, 2001; Donoghue & Smith, 2004), large-scale intra-continental disjunctions have received less attention in biogeography but they are especially relevant in the context of ecological vicariance. They are often explained by major environmental changes that fragment a continuously distributed lineage range, resulting in disconnected relict populations with independent evolutionary trajectories at each side of the disjunction (Axelrod & Raven, 1978; Crisp & Cook, 2007; Mairal *et al.*, 2015). In that situation, it is assumed that species migrate and conserve their climatic niche rather than evolve *in situ*. Recent phylogenetic studies show that phylogenetic niche conservatism (PNC) is a prevalent pattern in species diversification (Prinzing *et al.*, 2001; Ackerly, 2003; Crisp *et al.*, 2009; Wiens *et al.*, 2010) and might play a major role into the process of disjunction (Wiens, 2004; Kozak & Wiens, 2010). In the context of climate-driven disjunction, under the paradigm of climatic niche conservatism (Wiens & Graham, 2005), species are expected to shift their range to track suitable conditions at a pace determined by their climatic tolerances.

One of the best examples of intra-continental disjunctions is the African Rand Flora (Christ, 1892). The name refers to an enigmatic biogeographical pattern in which distantly related plant lineages share a similar disjunct distribution at the margins of the African continent and adjacent islands (between Macaronesia–north-west Africa, Horn of Africa–South Arabia–Socotra Island, Eastern Africa–Madagascar and South Africa (Bramwell, 1985; Andrus *et al.*, 2004; Sanmartín *et al.*, 2010; Pokorný *et al.*, 2015). The word ‘Rand’ originates from the German for edge or rim and refers to the fact that these lineages now occupy geographically isolated

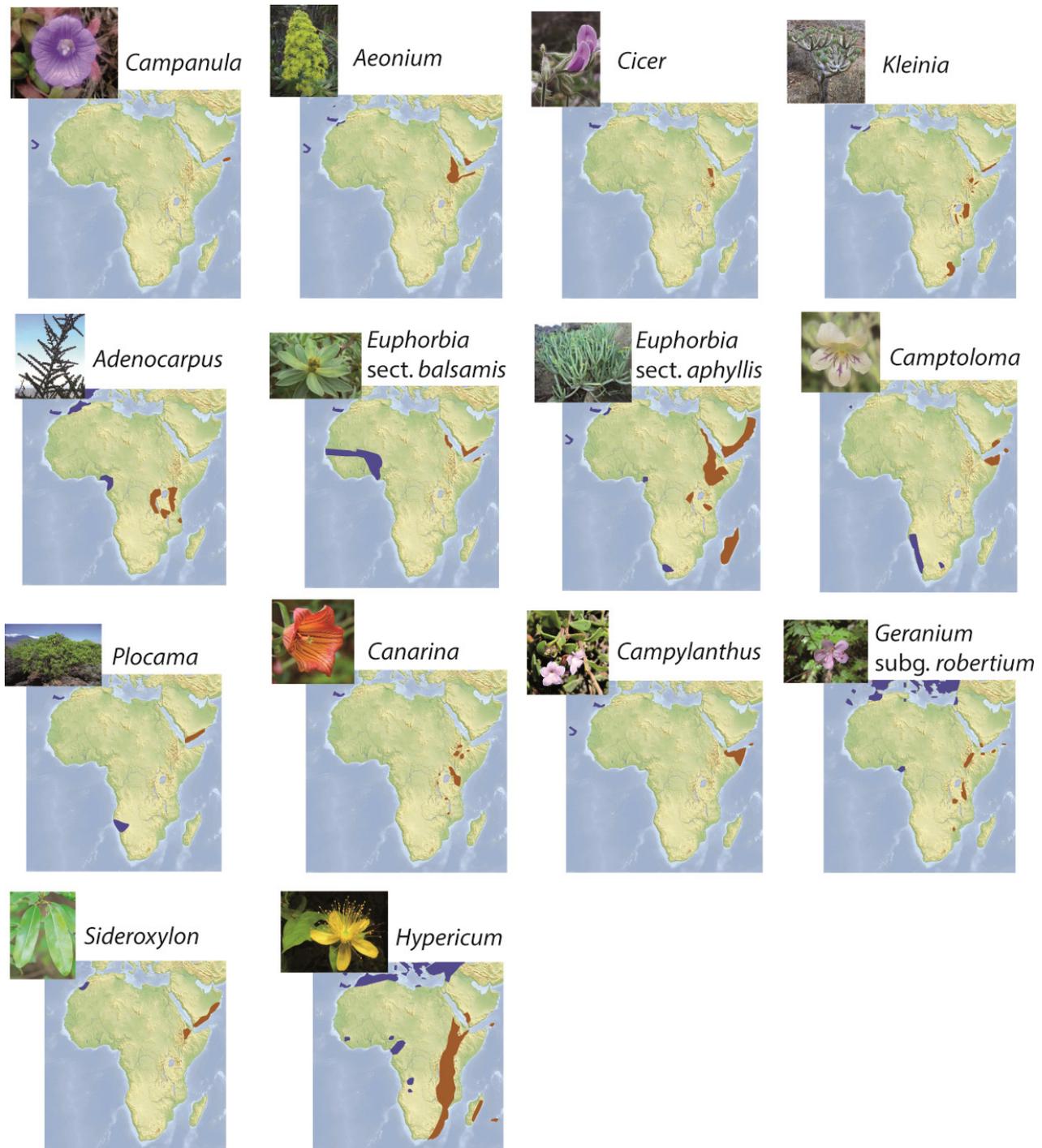
regions in the continental margins of Africa, forming a ring and leaving the centre of the continent ‘hollow’ (Pokorný *et al.*, 2015). Although Rand Flora lineages differ in their ecological affinities – some are adapted to subtropical conditions, others exhibit more xeric affinities, and some can be found in the Afrotropical mountain regions – none of them are adapted to desert or rain forest habitats. Therefore, the tropical lowlands of Central Africa (Guineo-Congolian region) and the Sahara and Sino-Arabic Deserts in the north or the Kalahari in the south act for them as effective ecological barriers to dispersal.

The Rand Flora pattern has traditionally been explained by vicariance of a once-continuous flora across North and Central Africa by climatic aridification events (vicariance–refugium hypothesis), which left geographically disjunct sister clades, for example, between Eastern Africa/South Arabia and north-west Africa/Macaronesia (Axelrod & Raven, 1978; Bramwell, 1985; Thiv *et al.*, 2010). At the start of the Neogene (25 Ma), Africa had a warm and humid climate and was covered by tropical forests and woodlands. Global climatic cooling after the mid-Miocene Climatic Optimum (MMCO, 17–14 Ma) – and a combination of factors, including the closing of the Tethys Seaway in the north and the tectonic uplift of Eastern Africa – triggered a gradual aridification process that proceeded from south-west to north, and which replaced the former forest by grasslands and savanna (Coetzee, 1993; Plana, 2004; Micheels *et al.*, 2009; Senut *et al.*, 2009). The onset of aridity in the Sahara did not start until the end of the Miocene, 7 Ma, but during the rapid climatic oscillations of the Plio-Pleistocene, the alternation of more humid periods with other drier periods might have favoured vegetation range expansion and fragmentation across North and Central Africa (Trauth *et al.*, 2009; see Pokorný *et al.*, 2015 for a more detailed description). The vicariance–refugium hypothesis has its counterpart in the idea that these disjunct distributions were formed in more recent times by independent long-distance dispersal (LDD) events, from north to south or south to north, followed by speciation *in situ* (del Hoyo *et al.*, 2009; Sanmartín *et al.*, 2010). LDD has been used to explain other examples of wide-range disjunctions in Africa (Coleman *et al.*, 2003; Calviño *et al.*, 2006; Pelsner *et al.*, 2012).

Testing the ecological vicariance–refugium hypothesis requires an accurate estimation of divergence times among the disjunct Rand Flora clades as well as of the climatic preferences of each lineage: When did they diverge? Under which climatic conditions could they maintain viable populations (Wiens, 2004)? Recently, Pokorný *et al.* (2015) answered one of these questions. Using time-calibrated molecular phylogenies, they estimated the age of the Rand Flora disjunction across 16 angiosperm lineages. Their results showed that many of these disjunctions fell within the Late Miocene-Pliocene period, after the onset of aridification in Africa, although some lineages exhibited older (mid-Miocene) and younger (Pleistocene) divergences.

Here, we investigated the relationship between the climatic tolerances of species and their age of divergence, using 14 lineages with disjunctions across the Saharo-Arabic Desert (Fig. 1, Table 1). First, we tested whether the tempo of vicariance between the disjunct western and eastern clades within each Rand Flora lineage is associated with the average values of the pooled climatic niche of the lineage. In a

situation of niche conservatism under shifting climatic conditions, the climatic preferences of lineages should have constrained the temporal sequence of divergence, with the most sensitive taxa diverging earlier and those more tolerant to the new climatic conditions diverging later. In contrast, if the climate niches are labile under the considered time frame, or if climate is changing along axes that are not



**Figure 1** Current geographical distribution of the 14 Rand Flora lineages used in this study. Distribution colours represent the disjunct clades at each side of the Sahara and whose climatic niches were modelled here: east (brown) and west (blue).

**Table 1** Selected Rand Flora lineages (from youngest to oldest) used in this study, exhibiting an east/west disjunction across the Sahara-Arabic Desert. For each lineage, the western and eastern disjunct clades, their species composition and age of divergence (mean and 95% HPD confidence interval, from Pokorný et al., 2015) are given.

Lineage	Western clade	Western geographical distribution	Eastern clade	Eastern geographical distribution	Age (Ma)	HPD (Ma)
<i>Campanula</i>	<i>C. jacobaea</i>	Cape Verde	<i>C. balfourii</i>	Socotra	1	0.4–1.7
<i>Aconitum</i>	<i>A. balsamiferum</i>	Canary Islands	<i>A. leucoblepharum</i>	East Africa	1.65	0.2–4.7
<i>Cicer</i>	<i>C. canariense</i>	Canary Islands	<i>C. cuneatum</i>	East Africa–South Arabia	3.43	0.6–7.8
<i>Kleinia</i>	<i>K. nerifolia</i> – <i>K. anteuophorbium</i>	Macaronesia	<i>K. anteuophorbium</i>	East Africa	3.57	2–6.9
<i>Adenocarpus</i>	3 Macaronesian species (e.g. <i>A. ombriosus</i> ) + <i>A. complicatus</i>	Macaronesia	<i>A. marnii</i>	Subtropical Africa	3.66	1.4–6.6
<i>Euphorbia</i> sect. <i>balsamis</i>	<i>E. balsamifera</i> ssp. <i>balsamifera</i>	Macaronesia–W. Africa	<i>E. balsamifera</i> ssp. <i>adenensis</i>	East Africa	3.8	1.4–7.1
<i>Camptoloma</i>	<i>C. canariense</i>	Canary Islands	<i>C. lyperijflorum</i>	Horn of Africa–South Africa	5.45	1.2–10.7
<i>Euphorbia</i> sect. <i>aphyllis</i>	12 sps. subsect. <i>macaronesicae</i> (e.g. <i>E. aphylla</i> )	Macaronesia	14 sps. subsect. <i>africanae</i> (e.g. <i>E. nubica</i> )	Central, East and South Africa	5.5	3.7–9.7
<i>Plocama</i>	<i>P. pendula</i>	Macaronesia	<i>P. tinctoria</i> – <i>P. yemenensis</i> – <i>P. crocyllis</i>	East Africa–South Arabia–South Africa	6.19	3–10.5
<i>Canarina</i>	<i>C. canariensis</i>	Macaronesia	<i>C. eminii</i>	East Africa	6.5	3.4–9.8
<i>Campylanthus</i>	<i>C. salsoloides</i> – <i>C. glaber</i>	Macaronesia	Remaining <i>Campylanthus</i> species	East Africa–Southern Arabia–Pakistan	7.5	3.1–14.2
<i>Geranium</i>	Nine species (e.g. <i>G. robertianum</i> )	Macaronesia–Morocco–Iberian Peninsula	Three species (e.g. <i>G. ocellatum</i> )	East Africa	11.04	7.6–15.4
<i>Sideroxylon</i>	<i>S. spinosa</i>	Argan sector (Morocco)	<i>S. mascatense</i>	East Africa–South Arabia	17.5	10–26.2
<i>Hypericum</i>	<i>H. androsaemum</i> – <i>H. grandifolium</i> – <i>H. hircinum</i> – <i>H. foliosum</i>	Macaronesia	<i>H. pamphylicum</i>	Turkey	17.3	9.5–25

relevant to the species, no relationship should be observed between the species climatic niche and the age of divergence. Second, to understand the spatiotemporal evolution of the Rand Flora disjunction, we modelled the climatic niche for each lineage, and used a combination of spatial distribution modelling techniques and palaeoenvironmental data to map their potential distribution across the past 17 Myr.

## MATERIALS AND METHODS

### Rand Flora lineages

We focused on 14 angiosperm plant lineages exhibiting a disjunction, at the level of species or clades of species (Fig. 1, Table 1), between both sides of the Saharo-Arabic desert: *Adenocarpus* DC. (Fabaceae), *Aeonium* Webb & Berth, *Campanula* L. (Crassulaceae), *Camptoloma* Benth. (Scrophulariaceae), *Campylanthus* Roth. (Scrophulariaceae), *Canarina* L. (Campanulaceae), *Cicer* L. (Fabaceae), *Euphorbia* L. sect. *balsamis*, *Euphorbia* L. sect. *aphyllis* (Euphorbiaceae), *Geranium* (Picard) Rouy (Geraniaceae), *Hypericum* L. (Hypericaceae), *Kleinia* Mill. (Astraceae), *Plocama* W. Aiton (Rubiaceae) and *Sideroxyon* L. (Sapotaceae). The selected lineages represent a geographical split between Eastern Africa (including the Eastern Arc Mountains, the Horn of Africa, the Socotra archipelago and southern Arabia) and Western Africa (including Macaronesia, the Atlas Mountains and region around the Cameroon volcanic line). All these lineages were included in the study by Pokorny *et al.* (2015) together with published molecular phylogenetic data that included nearly complete taxon sampling. Divergence times were estimated using a Bayesian relaxed clock, with absolute ages calibrated with the fossil record or secondary age constraints obtained from a more inclusive phylogenetic analysis; see Pokorny *et al.* (2015) for more details. Current distributions, dated chronograms of all 14 lineages indicating their distribution, phylogenetic relationships, dating uncertainty and the disjunct node of interest (i.e. the divergence between the north-western/eastern clades) are shown in Fig. 1 and in Figure S1.1 (see Appendix S1 in Supporting Information).

### Occurrences and environmental data

We collected species occurrence data covering the entire distributional range of the disjunct species/clades within each Rand Flora lineage. These were obtained from published monographs and inventories, online databases ([www.jardincanario.org/flora-de-gran-canaria](http://www.jardincanario.org/flora-de-gran-canaria); [www.gbif.org](http://www.gbif.org), [www.anthos.es](http://www.anthos.es)) and georeferenced populations collected during several fieldtrips between 2010 and 2014 (Madeira, Canary Islands, Cape Verde, Morocco, Iberian Peninsula, Ethiopia, Kenya, Uganda and Madagascar). In total, 4286 georeferenced localities were collated. Coordinates were checked by projecting them on the appropriate geographical map and then

eliminating localities of questionable reliability. The availability of thousands of georeferenced extant occurrences allowed us to quantify the climatic variables that limit the geographical distribution of the disjunct Rand Flora clades. We used the 19 bioclimatic variables available from WorldClim (at a resolution of 30 arc-seconds; [www.worldclim.org](http://www.worldclim.org); Hijmans *et al.*, 2005) and extracted the values of these variables for each occurrence of the disjunct species in each Rand Flora lineage. We did this separately for each bioclimatic variable and computed the mean for each species.

### Climatic niche and age of divergence

We investigated whether past climate change drove population divergence in Rand Flora lineages along a temporal sequence that was correlated to their climatic niche: if climate change is gradual over time, the age of the divergence tempo of vicariance should be correlated with the lineage climatic tolerance. Using a linear model, we estimated the relationship between the age of divergence of the eastern and western clades in each Rand Flora lineage and the mean climatic niche of the lineage (i.e. the two clades pooled) from the bioclimatic variables. We also evaluated whether a quadratic term provided a better fit of the relationship to the data than a linear model using the Akaike information criterion (AIC). Ecological impact of climate change over time may begin with mild changes and accelerate over time, which might generate a nonlinear relationship between the climatic niche and age of divergence. To control for false discovery rate, we applied corrections to the *P*-values associated to our regression linear model and the quadratic term, using the R package 'fdrtool' (Strimmer, 2008).

While a significant relationship between age of divergence and climatic niche would provide evidence consistent with niche conservatism, we performed an additional analysis to evaluate this assumption. For each bioclimatic variable, we evaluated whether the climatic niche variation was lower among species belonging to the same lineage (e.g. between *H. pamphylicum* and *H. grandifolium*) than among species belonging to different lineages irrespective of the side of the disjunction (e.g. between *H. grandifolium* and *Plocama pendula*). For those variables showing a significant association with age of divergence in the previous analysis, we computed the average niche value for each disjunct Rand Flora species. We then computed the difference in the average niche value between all sister taxa and tested whether the difference is lower within than between lineages using a Mantel test. For each climatic variable, we plotted the niche difference within the same Rand Flora lineage and across different Rand Flora lineages; if the second is consistently larger than the first across variables, this would support PNC. Finally, we performed a principal component analysis (PCA) with all climatic variables to quantify the degree of climatic niche overlap between the east/west disjunct sister taxa in relation to all other species in the genus/lineage.

## Species distribution modelling

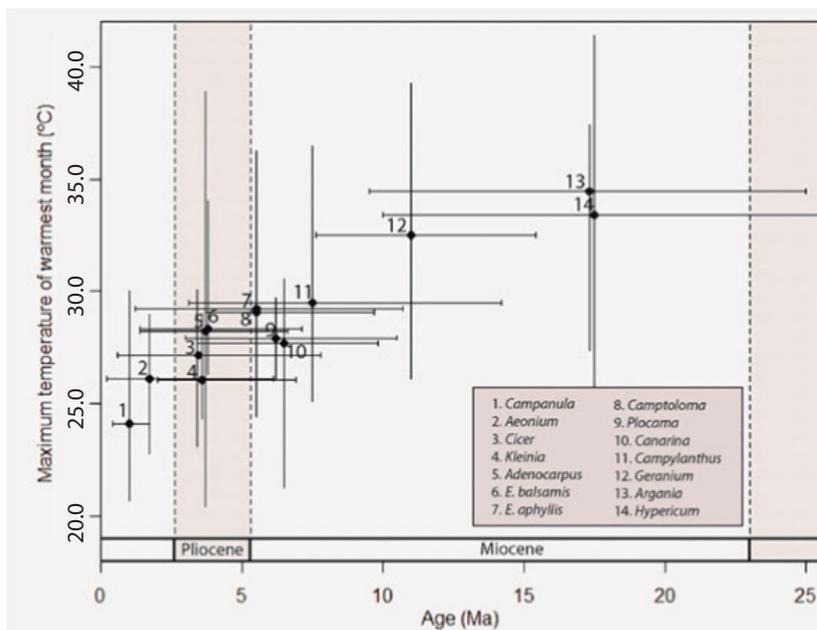
To model the present and past distribution of clades, we combined the available occurrences for the species within each lineage with a set of six bioclimatic variables for which estimates were available for the past: total annual precipitation, maximum and minimum monthly precipitation, annual mean temperature, and maximum and minimum monthly temperature. We ran the analyses considering 2- to 4-month periods that cover the two seasons with more accentuated differences in precipitation: November to February and June to September. Pseudoabsences were generated by selecting 5000 random points across Africa, as suggested in Wisz & Guisan (2009). We used ensemble modelling to generate our predictions. This procedure integrates the results from multiple modelling techniques within an ensemble hindcasting framework to achieve more robust hindcasts (Araújo & New, 2007). Four modelling techniques, generalized linear models, generalized additive models (GAM), general boosting method (GBM) and random forests, were run and summarized using R packages (R Core Team, 2014): 'biomod2' (Thuiller *et al.*, 2013), 'foreign', 'raster' (Hijmans & van Etten, 2016), 'SDMTools' (VanDerWal *et al.*, 2011), 'rms' (Harrell, 2016), 'gbm' (Ridgeway, 2015), 'gam' (Hastie, 2016), 'rJava' (Urbanek, 2010), 'dismo' (Hijmans *et al.*, 2016) and 'randomForest' (Liaw & Wiener, 2002) with default settings. For past climate simulations, we used four global Hadley Centre general circulation models (HadCM3L) that incorporate the effect of changes in atmospheric CO<sub>2</sub> and represent major climate (warming or cooling) events worldwide in Africa (Meseguer *et al.*, 2015): a 400 p.p.m. CO<sub>2</sub> Late Miocene simulation representing the early warm period of the MMCO, a 280 p.p.m. CO<sub>2</sub> Late Miocene simulation representing the cold and dry conditions prevalent after the Late Miocene

Cooling (LMC) event (c. 11.6–5.3 Ma) and a 560 p.p.m. CO<sub>2</sub> Pliocene simulation representing the conditions at the Mid-Pliocene Warming Event (MPWE; 3.6 Ma) and a simulation of the Preindustrial World with 280 p.p.m. CO<sub>2</sub> to provide a baseline HadCM3L climate before the industrial revolution. Details of the HadCM3L model setup for the palaeoclimate simulations are given in Meseguer *et al.* (2015).

## RESULTS

### Climatic niche and age of divergence

We found significant relationships between the climatic niche of the lineages (i.e. the eastern and western clades pooled) and the age of the divergence between the two clades. The group of bioclimatic variables related to temperature showed the highest coefficient of determination. Maximum temperature of the warmest month showed the best fit (Fig. 2:  $R^2 = 0.883$ ; slope = 0.165), followed by other variables related to temperature, such as mean diurnal range ( $R^2 = 0.8081$ ; slope = 0.001) and mean temperature of the warmest quarter ( $R^2 = 0.768$ ; slope = 0.239) (Table 2). In contrast, precipitation variables had low values of coefficient of determination. These results were corroborated by the models adding a quadratic term, which showed a smaller AIC value for the variables with the highest coefficient of determination (maximum temperature of the warmest month  $55.56 < 60.61$ ; mean diurnal range  $63.58 < 67.54$ ; mean temperature of the warmest quarter  $61.44 < 70.2$ ; see Table 2). Supplemental plots for all climate variables are shown in Figure S1.2. Overall, the oldest lineages showed climatic tolerances to warmer climates (e.g. *Sideroxylon*, *Hypericum*), while younger divergences were correlated to more



**Figure 2** For each Rand Flora lineage analysed here, the age of divergence (in Ma) between the western and eastern disjunct clades is plotted against their climatic optimum for the maximum temperature of the warmest month (in °C). Bars in the x-axis show the 95% HPD confidence intervals for the age estimates (full circles represent the mean estimates). Bars in the y-axis show the 5% and 95% quantiles for the temperature range.

**Table 2** Statistical relationships between the age of divergence of the eastern and western clades (Table 1) and the mean climatic niche of the lineage (the two clades pooled);  $R^2$ : coefficient of determination obtained using a linear model. Also shown are the results of the models including both linear and quadratic terms. AIC, Akaike information criterion.

Bioclim variable	$R^2$	Linear term	AIC	Linear term	Quadratic term	AIC
Maximum temperature of warmest month	0.8831	0.165	60.61	0.9165	4.68E-07	55.56
Mean diurnal range	0.8081	0.0001	67.54	0.8519	1.09E-05	63.58
Mean temperature of warmest quarter	0.7681	0.2395	70.2	0.8729	4.72E-06	61.44
Temperature annual range	0.7442	0.0015	71.57	0.7029	0.0005032	73.33
Annual mean temperature	0.3203	0.034	85.25	0.2455	0.0853	86.39
Temperature seasonality	0.2921	0.046	85.82	0.3444	0.09808	86.75
Mean temperature of wettest quarter	0.2691	0.0573	86.27	0.2164	0.1044	86.9
Mean temperature of driest quarter	0.1703	0.1425	90.63	-0.116	0.7296	91.85
Precipitation of driest month	0.165	0.1496	88.13	0.1953	0.1208	87.28
Mean temperature of coldest quarter	0.155	0.1637	90.55	0.6825	0.0007259	74.26
Precipitation of coldest quarter	0.1451	0.179	88.46	0.03738	0.3236	89.78
Precipitation of wettest quarter	0.1164	0.2326	88.92	0.124	0.1926	88.46
Precipitation of wettest month	0.1005	0.2694	89.17	0.101	0.2221	88.83
Minimum temperature of coldest month	0.0765	-0.0497	88.3	0.2705	0.07041	85.9
Precipitation of warmest quarter	0.0685	0.366	89.66	0.1784	0.1354	87.57
Annual precipitation	0.042	0.2339	88.93	-0.04497	0.5082	90.93
Precipitation seasonality	0.0177	0.064	90.41	-0.1227	0.7542	91.94
Isothermality	0.017	0.6565	90.42	0.1194	0.1983	88.54
Precipitation of driest quarter	0.0016	0.8915	88.04	0.1389	0.1753	88.22

temperate or arid climatic preferences (Fig. 2). The Mantel test indicated a statistically significant positive relationship between the climatic and phylogenetic matrices for the majority of variables (Table 3), although this number decreased after applying the Bonferroni correction. Similarly, plotting the median and quartile ranges for these variables showed that the within-lineage difference for niche values was lower than the difference across lineages (Figure S1.3). Although the Bonferroni correction is often considered to be too conservative, we noted that the variables showing the lowest  $P$ -value (Table 3) did not always show the largest statistical correlation to the age of divergence (Table 2, 3). Finally, the PCA analysis (Figure S1.4) showed that the degree of overlap in climatic niche space between the east/west disjunct sister taxa is comparable to the one found in the remaining species in the lineage/genus; even those with less overlap between east and west (e.g. *Campylanthus*) showed values falling within the genus climatic niche space.

### Species distribution modelling

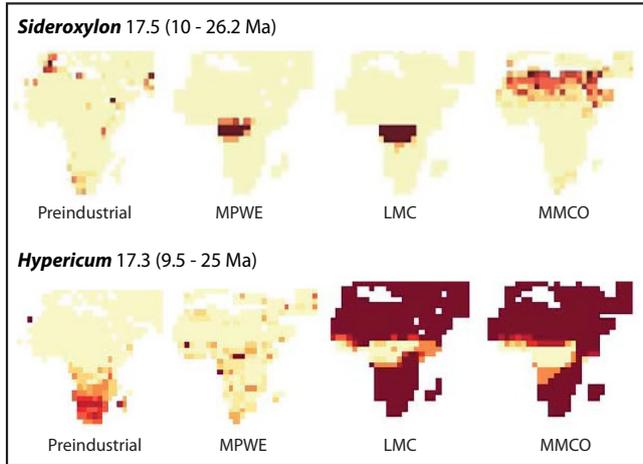
Species distribution models and palaeoenvironmental data indicated a general decrease in climatic suitability through time for most species since the mid-Miocene (Fig. 3). Interestingly the MMCO showed suitable projections for mid-Miocene groups (*Hypericum* and *Sideroxylon*; Fig. 3a), perhaps signalling that these groups are more ancient and paratropical. Projections in the Late Miocene period, representing a global cooling event, revealed wide distribution ranges with connections joining the east and west edges of Africa. Several clades, whose divergences date back to the Late Miocene-Zanclean period (11.67–3.6 Ma; Fig. 3b), are shown to have suitable ranges connecting Eastern and Western Africa with

**Table 3** Mantel test results to assess whether within-lineage difference in climatic values is lower than the difference across lineages for each bioclimatic variable. \*Variables that remain significant after Bonferroni test correction.  $Q$ -values are the false discovery rate-adjusted  $P$ -values.

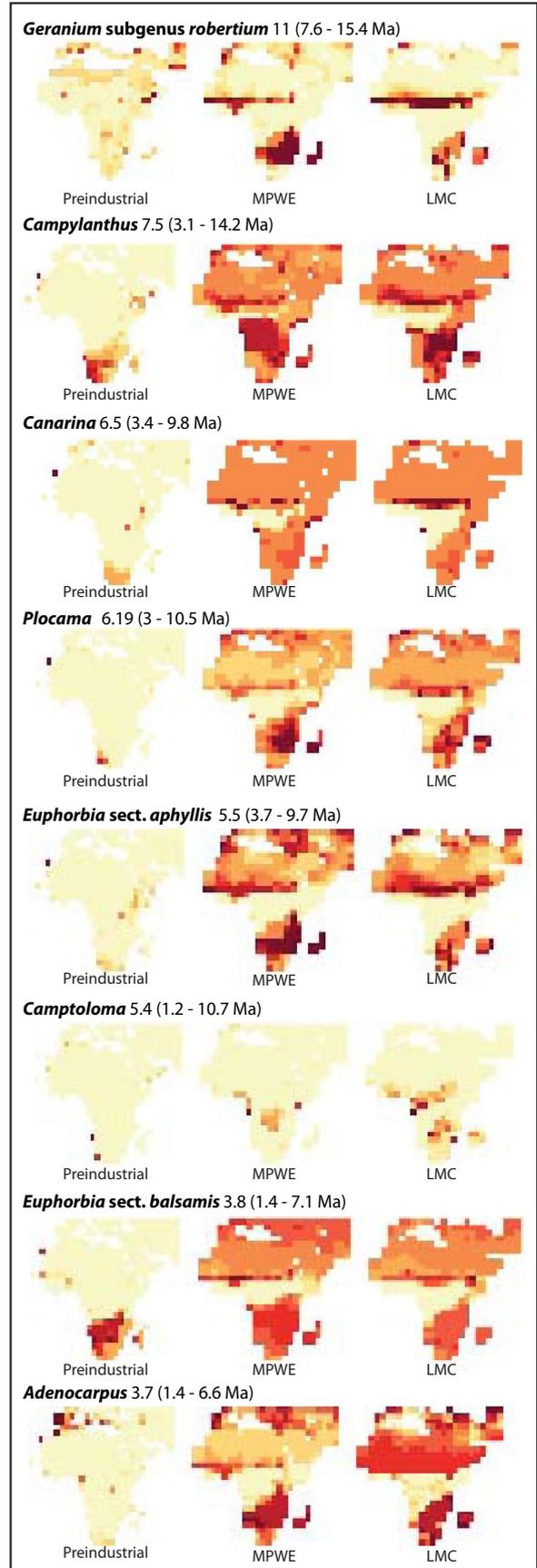
Bioclim variable	Z-statistics	$P$ -value	$Q$ -value
Annual mean temperature	530.15	0.001*	0.016
Mean diurnal range	38.56	0.009	0.035
Isothermality	174.76	0.001*	0.007
Temperature seasonality	268.83	0.071	0.004
Maximum temperature of warmest month	588.57	0.099	0.034
Minimum temperature of coldest month	841.12	0.015*	0.18
Temperature annual range	102.32	0.637	0.045
Mean temperature of wettest quarter	609.543	0.001*	0.025
Mean temperature of driest quarter	510.66	0.003	0.062
Mean temperature of warmest quarter	459.09	0.005	0.188
Mean temperature of coldest quarter	778.52	0.001*	0.002
Annual precipitation	777.96	0.135	0.011
Precipitation of wettest month	142.78	0.051	0.18
Precipitation of driest month	218.35	0.481	0.067
Precipitation seasonality	412.16	0.781	0.002
Precipitation of wettest quarter	362.86	0.043	0.013
Precipitation of driest quarter	797.67	0.433	0.034
Precipitation of warmest quarter	217.26	0.169	0.04
Precipitation of coldest quarter	263.48	0.509	0.142

an environmentally suitable corridor south of the Sahel (e.g. *Geranium* subgenus *Robertium*, *Plocama*, *Canarina*, *Campylanthus*, *Euphorbia* sect. *balsamis*, *Euphorbia* sect. *aphyllis*,

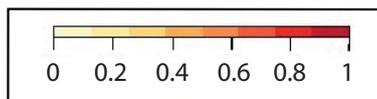
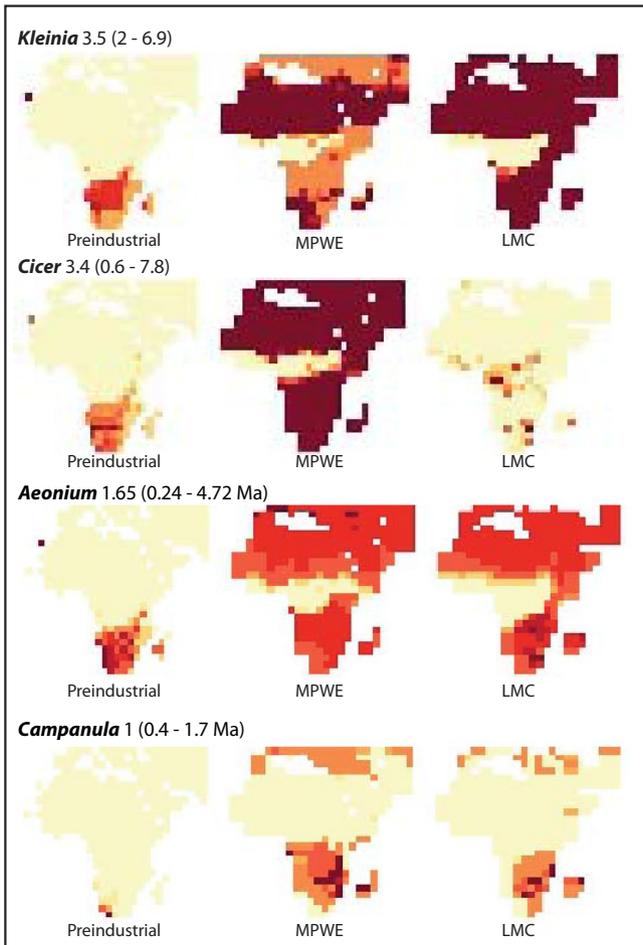
a) Mid Miocene groups



b) Late Miocene - Zanclean groups



c) Piacenzian - Pleistocene groups



**Figure 3** Geographical projection of the climatic niche of Rand Flora lineages over four different palaeoclimate simulations representing major warming or cooling events in the Late Cenozoic Earth history (Meseguer *et al.*, 2015). Reconstructions are grouped into three geological periods according to the estimated age of the disjunction (Table 1): (a) mid-Miocene groups (17–14 Ma); (b) Late Miocene–Zanclean groups (11.6–3.6 Ma) and (c) Piacenzian–Pleistocene groups (3.6–0.12 Ma). For each lineage, mean age of divergence between the western and eastern clades is shown in million years (Ma) with the 95% HPD confidence interval in parentheses (Table 1). Abbreviations for palaeoclimatic layers: MMCO (Mid-Miocene Climatic Optimum: 17–14 Ma), LMC (Late Miocene Climate cooling: 11.6–5.3 Ma), MPWE (Mid-Pliocene Warming Event: 3.6 Ma) and Preindustrial (Preindustrial world, < 1900). Colours in the bar at the bottom left indicate the climatic suitability likelihood for the presence of each clade and according to its climatic tolerance range: soft yellow colours indicate low climatic suitability values, while dark red indicates high suitability regions.

*Adenocarpus*). In the mid-Pliocene simulation (representing a major warming event), the predicted potential distribution shows wider disjunctions that split the suitable range for these taxa on either side of the continent. Other lineages with younger divergences show broad disjunctions and high suitability values during the mid-Pliocene (*Kleinia*, *Cicer*, *Aeonium*). In general, hindcasted models showed wider suitable ranges for Rand Flora species in North and Central Africa in the past before the aridification of the Sahara as compared to their current disjunct distributions.

## DISCUSSION

Under the PNC hypothesis (Donoghue, 2008), it has been proposed that species should retain similar environmental niches over evolutionary time scales (niche conservatism, Wiens & Graham, 2005; Wiens *et al.*, 2010) and that this constraint should modulate the rate of speciation of clades (Wiens, 2004). Species failure to adapt to new environmental conditions should isolate populations on peripheral locations, which would trigger the formation of new lineages. A significant relationship between the time-since-speciation and the environmental niche of sister taxa is expected to provide clues on the role of niche conservatism in driving speciation (Pyron *et al.*, 2014).

### Tempo of vicariance and climatic niche

We found a strong positive correlation between the time of divergence of sister-species/clades distributed in Macaronesia–NW Africa and Eastern Africa–Arabia and the mean climatic niche of the Rand Flora lineages (Table 2). This suggests that niche conservatism, manifested by the failure of a species to adapt to increasingly arid conditions in North Africa, starting around the mid-Late Miocene (Pokorný *et al.*, 2015), likely drove the initial splitting of allopatric lineages. In addition to the lineages studied here, other examples of biotic disjunction between the edges of the African continent have been described in vascular plants (Sanmartín *et al.*, 2010), vertebrates (Clouet & Wink, 2000; Lorenzen *et al.*, 2012) and invertebrates (Opatova & Arnedo, 2014). Therefore, in the context of Saharan desertification, our results support the hypothesis of large-scale niche conservatism (Crisp *et al.*, 2009), in which species generally retained their ancestral environmental constraints and shifted

their range at a pace matching their climatic niche, thus initiating vicariance and speciation.

Those Rand Flora lineages characterized by the highest values of maximum temperature of the warmest month (Fig. 2), and therefore more subtropical climatic niches, had the earliest split between eastern and western African clades (e.g. *Sideroxylon*, *Hypericum*). This fits with the evolutionary history of these lineages, which have been postulated to have originated from ‘boreotropical’ ancestors, that is, Holarctic origins from tropical ancestors in Early Cenozoic times when tropical climates were widespread across North America and Europe (Smedmark & Anderberg, 2007; Meseguer *et al.*, 2013). The next clades with ancient age of divergence are characterized by more temperate or subxeric affinities (e.g. *Canarina*, *Geranium*, *Campylanthus*, *Plocama*). In contrast, groups such as *Kleinia* (Fabaceae) or *Aeonium* (Crassulaceae) show younger splits and adaptations to drier habitats (Fig. 2). Thus, the sequence of splits in Rand Flora lineages seems to match the lineage climatic niches, following the gradual aridification of North Central Africa, with younger divergences corresponding to arid-adapted lineages. The fact that we found a slightly better fit with a quadratic model for the most informative variables suggests that the effect of climate change on species divergence might have accelerated through time.

These results corroborate the links between niche conservatism and speciation during environmental changes, in the context of ecological vicariance (Wiens, 2004). If climate change is fast and widespread, so that species have no time to adapt to new conditions, populations will either go extinct or be constrained to move and track suitable areas (Futuyma, 2010; Waldron, 2010). The species geographical range becomes fragmented into smaller refugia where populations persist, followed by local speciation (Wiens, 2004). This results in a common signature of vicariance across several unrelated lineages. The Australian flora offers such a case, where the formation of the arid Nullarbor Plain produced a congruent molecular signature of geographical division across multiple plant clades (Crisp & Cook, 2007). In a different situation, Pellissier *et al.* (2013) showed that Arctic-Alpine disjunct species retained their climatic tolerance after the Quaternary glacial period, which may lead to local vicariant speciation. On the other hand, if climate change is labile, with oscillations in different directions, or follows a spatial gradient, one would expect to see a pattern of niche

evolution with the two clades at each extreme side of the disjunction adapted to different climate optima (adaptation). We did not see this pattern here: the climatic preferences of the eastern and western clades did not show a significant degree of divergence compared with the rest of species in the genus. We also found differences in climatic affinities between genera larger than within each genus, which provides support to our assumption of PNC. Finally, if climate change is gradual or accelerating in one direction as along a temporal temperature gradient, one would expect to see a pattern, where species will conserve their ancestral climatic preferences rather than adapt to the new conditions. This would result in a predictable pattern (Donoghue & Edwards, 2014) of biogeographical 'pseudocongruence' (Pokorný *et al.*, 2015): the timing of vicariance events should match the lineage climatic tolerance, with a positive relationship between the age of the disjunction event and the species climatic niche as found in this study.

### Is vicariance linked to niche conservatism and persistence in refuges?

The species distribution modelling hindcasted to the reconstructed past climates showed generally broad geographical ranges for Rand Flora lineages in the Late Miocene, but a much more restricted current distribution. The colder and wetter climate of the Late Miocene resulted in favourable conditions for species, probably allowing continuous gene flow throughout North Africa. For many lineages, a climatic corridor of suitable environment can be observed south of the Sahel, connecting Eastern and Western Africa. The existence of this past climatic corridor agrees well with the study by Sanmartín *et al.* (2010), which demonstrated historically high rates of dispersal or biotic connection between north-west Africa–Macaronesia and Eastern Africa–Southern Arabia. As the climate became drier with more extreme temperature maxima towards the mid-Pliocene – which also coincided with a period of intense uplift in Eastern Africa (Sepulchre *et al.*, 2006) – species ranges contracted (Fig. 3) and central North Africa became unsuitable for most lineages. Interestingly, the opposite pattern can be observed for Holarctic groups, where the LMC event was responsible for large geographical disjunctions across North American and European temperate forests, whereas the subsequent increase in temperature at the mid-Pliocene warming interval allowed some of these forest taxa to regain a more widespread distribution (Sanmartín *et al.*, 2001; Meseguer *et al.*, 2015).

The gradual aridification resulted in lineages tracking suitable climatic conditions to have distributions restricted to climatic refugia in the east and western edges of Africa (e.g. the Afromontane region) and adjacent oceanic and continental islands (Macaronesia, Socotra). These areas conserved more subtropical or temperate habitats, due to topographic features (high altitude) or the mild influence of oceanic climates. Indeed, these regions have long been considered to

represent the actual refugia of the last remnants of subtropical flora that covered North Central Africa (Axelrod & Raven, 1978), in the Afromontane archipelago of East Africa and the laurisilva forest in Macaronesian archipelagos (though the latter has been challenged by recent phylogenetic work, Kondraskov *et al.*, 2015).

Species distribution modelling hindcasted to past climate is based on the premise that extant species share the same climatic preferences as their extinct ancestors. Although this might be true for short time scales, it is less likely for geological time scales of millions of years, especially under a scenario of rapid climatic oscillations as the Cenozoic (Stigall, 2012). In the absence of fossil data to reconstruct ancestral climatic preferences (see Meseguer *et al.*, 2015), this seems an unavoidable assumption. On the other hand, large-scale PNC has been argued for angiosperms (Crisp *et al.*, 2009), based on evidence that biome shifts are rare both within continents and in transoceanic colonizations – probably because these transitions often require the development of complex physiological adaptations (e.g. Donoghue, 2008). In our study, niche conservatism is supported by the finding of lower variance within than across lineages and by the strong positive relationship between time from divergence and the lineage mean climatic niche. Thus, our study supports the hypothesis that the variation in lineage tolerance to environmental conditions played a key role in the processes that created the Rand Flora biogeographical pattern.

Overall, our results provide support to the vicariance–refugium hypothesis as an explanation of the Rand Flora disjunction: the ancestors of Rand Flora lineages had in the past a more widespread distribution across North Africa, which became fragmented as a result of the increasing aridification of the continent from the Miocene onwards. The fact that these widespread distributions are not all of the same age (Fig. 2) lends support to the idea that the Rand Flora pattern was not formed by a single vicariance event but originated at different times during episodes of global drought during the Miocene–Pliocene (Pokorný *et al.*, 2015). Our projections (Fig. 3) do not allow us to discard the possibility that some Rand Flora lineages never actually had a continuous distribution from west to east North Africa. The presence of patches of climatic suitability in MPWE palaeoclimate reconstructions suggests the possibility of stepping stones or climatic refuges facilitating migration across the Sahara during climatically unfavourable periods for at least some of these lineages.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Supplementary figures.

## BIOSKETCHES

**Mario Mairal's** research is focused on macroevolution and microevolution in island systems, with special focus in the biogeography and ecology of the Rand Flora pattern.

**Isabel Sanmartín** is a senior researcher at the Real Jardín Botánico, CSIC (Madrid, Spain). Her main research interests include the study of large-scale biogeographical patterns and the development of analytical inference methods with special reference to model-based approaches.

**Loïc Pellissier** is Assistant Professor in Landscape Ecology and investigates how past landscape changes have influenced species distributions to guide future forecast of biodiversity responses to global changes.

Author contributions: M.M., I.S. and L.P. designed the study; M.M. and I.S. gathered the data; M.M. and L.P. analysed the data; M.M., I.S. and L.P. led the writing.

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