Leaps and bounds: geographical and ecological distance constrained the colonisation of the Afrotemperate by *Erica*

Pirie, M.D. [1, 2, 3, 8], Kandziora, M. [1,4], Nürk, N.M. [5], Le Maitre, N.C. [2], Mugrabi de Kuppler, A. [6], Gehrke, B. [1], Oliver, E.G.H. [7], and Bellstedt, D.U. [2]

Author affiliations

[1]Institut für Organismische und Molekulare Evolutionsbiologie, Johannes Gutenberg-Universität, Anselm-Franz-von-Bentzelweg 9a, 55099 Mainz, Germany

[2]Department of Biochemistry, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa

[3]University Museum of Bergen, University of Bergen, Bergen, Norway

[4]Life and Environmental Sciences, School of Natural Sciences, University of California, Merced, USA

[5]Institute of Plant Systematics, Bayreuth Centre of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstraße 30, 95447 Bayreuth, Germany

[6]INRES Pflanzenzüchtung, Rheinische Friedrich-Wilhelms-Universität Bonn, Katzenburgweg 5, 53115 Bonn, Germany

[7]Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa

[8]Author for correspondence: pirie@uni-mainz.de; phone: +49 6131 3922928

Abstract

The coincidence of long distance dispersal and biome shift is assumed to be the result of a multifaceted interplay between geographical distance and ecological suitability of source and sink areas. Here, we test the influence of these factors on the dispersal history of the flowering plant genus *Erica* (Ericaceae) across the Afrotemperate. We quantify similarity of *Erica* climate niches per biogeographic area using direct observations of species, and test various colonisation scenarios while estimating ancestral areas for the *Erica* clade using parametric biogeographic model testing. We infer

that the overall dispersal history of *Erica* across the Afrotemperate is the result of infrequent colonisation limited by geographic proximity and niche similarity. However, the Drakensberg Mountains represent a colonisation sink, rather than acting as a "stepping stone" between more distant and ecologically dissimilar Cape and Tropical African regions. Strikingly, the most dramatic examples of species radiations in *Erica* were the result of single unique dispersals over longer distances between ecologically dissimilar areas, contradicting the rule of phylogenetic biome conservatism. These results highlight the importance of rare biome shifts, in which a unique dispersal event fuels evolutionary radiation.

Keywords: Afrotemperate; historical biogeography; phylogenetic biome conservatism; Cape Floristic Region; climatic niche shift; *Erica*; evolution; Madagascar; model testing

Introduction

The current day distributions of many plant groups are the result of long distance dispersal (LDD) (Muñoz et al., 2004; Alsos et al., 2007; Kadereit & Baldwin, 2012; Ruhfel et al., 2016; Jordano, 2017). Such events are thought to be rare (Nathan, 2006; but see Viana & al., 2015), but rarer still might be plant dispersals across long distances between different biomes (Crisp et al., 2009). The coincidence of intercontinental dispersal and biome shift, such as inferred in *Lupinus* (Drummond et al., 2012), *Bartsia* (Uribe-Convers & Tank, 2015), and *Hypericum* (Nürk, Michling & Linder, 2018), is assumed to be the result of a multifaceted interplay between geographical distance and ecological suitability of source and sink areas (Donoghue & Edwards, 2014). Here, we test the influence of these factors on the biogeographic history of the flowering plant genus *Erica* (Ericaceae).

The more than 800 *Erica* species across Europe and Africa provide an excellent example with which to test the impact of geographical and ecological distance on biogeographic history. Just 21 of the species are found in Central and Western Europe, Macaronesia, the Mediterranean and the Middle East. This species-poor assemblage nevertheless most likely represents the ancestral area of the clade (McGuire & Kron, 2005; Mugrabi de Kuppler et al., 2015; Kowalski & Fagúndez, 2017) where the oldest lineages began to diversify c. 30 Ma (Pirie et al., 2016). From around 15 Ma, a single lineage dispersed across different biomes of the Afrotemperate (sensu White, 1981): today 23 species are known from the high mountains of Tropical Africa; 51 in Southern Africa's Drakensberg Mountains; c. 41 in Madagascar and the Mascarene islands; and c. 690 in the Cape Floristic Region of South Africa (Oliver, 2012; Pirie et al., 2016). Present day habitats of *Erica* species tend to be low nutrient and fire prone (Ojeda, 1998), but hence still differ markedly in ecology, from the

63 Mediterranean climates of southern Europe and the Cape to colder climes of northern Europe and
64 the non-seasonal temperate habitats of the high mountains in Tropical Africa. These habitats are also
65 separated by considerable geographic distances, isolated by expanses of inhospitable ecosystems
66 and/or ocean. Nonetheless, similar distribution patterns across Europe and Africa are observed in
67 different plant groups (e.g. Galley et al., 2007; Gizaw et al., 2016).

68 Organisms adapted to different habitats respond differently to changing environmental conditions
69 (Mairal, Sanmartín & Pellissier, 2017; Chala et al., 2017). For example, plant groups with greater
70 tolerances of aridity than *Erica* may have had more contiguous past distributions across Africa
71 (Bellstedt et al., 2012). Similar distribution patterns of such groups might thus be best described by
72 biogeographic scenarios emphasising vicariance processes, such as for example the "Rand Flora",
73 representing plant lineages that show similar disjunct distributions around the continental margins of
74 Africa (Sanmartín et al., 2010; Pokorny et al., 2015), or the "African arid corridor" hypothesis that
75 seeks to explain disjunct distributions between the Horn of Africa and arid south-western Africa
76 (Verdcourt, 1969; White, 1983). By contrast, similar distribution patterns observed across plants such
77 as *Erica* that are adapted, or otherwise restricted, to habitats that remained largely isolated over
78 time might instead be explained by concerted patterns of LDD (Knox & Palmer, 1998; Galbany-Casals
79 et al., 2014; Nürk et al., 2015; Míguez et al., 2017). Examples include the shared arid adapted
80 elements of Macronesia and adjacent North-West Africa and Mediterranean (Kim et al., 2008;
81 Fernández-Palacios et al., 2011; García-Aloy et al., 2017), and the more mesic temperate or tropical
82 alpine habitats of the "sky islands" of East Africa, in which, for example, multiple lineages originated
83 from northern temperate environments (Gehrke & Linder, 2009; Gizaw et al., 2013, 2016).

84 A more specific biogeographic scenario, inferred from Cape clades with distributions very similar to
85 that of *Erica,* involves dispersal north from the Cape to the East African mountains via the
86 Drakensberg ("Cape to Cairo"; Galley & al., 2007). McGuire & Kron (2005) proposed a different
87 scenario for *Erica* instead: southerly stepping stone dispersal through the African high mountains to
88 the Cape. Both scenarios, however, imply that dispersal is more frequent between adjacent
89 areas/over shorter distances. Short distance or stepping stone dispersal may indeed be more
90 probable than LDD (Nathan, 2006), and distance alone could conceivably be more important than
91 directionality (Linder et al., 2013). On the other hand, the probabilities of LDDs are hard to model
92 (Higgins & Richardson, 1999; Nathan, 2006), in part because (observable) LDD events also involve
93 successful establishment in more or less distinct environments (Donoghue & Edwards, 2014). Thus
94 geographic distance and ecological suitability might individually constrain the biogeographic history
95 of plants, or the interplay between both factors may be decisive (Donoghue, 2008; Carvajal-Endara et
96 al., 2017), so much so that clades with similar ecological tolerances and origin might show

97 convergence to similar distribution patterns (Merckx et al., 2015; Gizaw et al., 2016; Mairal,
98 Sanmartín & Pellissier, 2017).

99 In this paper, we ask whether and to what extent geographic proximity or climatic niche similarity
100 constrained the colonisation of the Afrotemperate by *Erica*. Until recent work (Pirie, Oliver &
101 Bellstedt, 2011; Pirie et al., 2016), too little was known of the phylogenetic relationships of the 97%
102 of *Erica* species outside Europe to be able to address such questions. Specifically, we test six
103 biogeographic models, as illustrated in Fig. 1: Three that test the influence of geographic distance,
104 climatic niche similarity, and the combination of both; and three differing stepping stone models that
105 each imply geographical distance effects promoting dispersal predominantly between adjacent
106 areas: northerly "Cape to Cairo", "Southerly stepping stone" and a model that invokes elements of
107 both, the "Drakenberg melting pot" hypothesis.

108

109 **Materials and Methods**

110 *Phylogenetic hypothesis:* Analyses were based on phylogenetic trees (Pirie et al., 2016) which
111 represent c. 60% of the c. 800 species of *Erica* from across their geographic range and DNA
112 sequences from multiple plastid markers (*trnT-trnL* and *trnL-trnF-ndhJ* spacer sequences for all taxa,
113 with exemplar sampling of *trnL* intron, *atpI-atpH* spacer, *trnK-matK* intron and *matK* gene, *psbM-trnH*
114 spacer, *rbcL* gene, *rpl16* intron, *trnL-rpl32* spacer sequences) and nuclear ribosomal (nrDNA) internal
115 transcribed spacer (ITS; for all taxa). For the biogeographic analyses here, we adopt the phylogenetic
116 hypothesis of Pirie et al. (2016), the best tree inferred under Maximum Likelihood (ML) using RAxML
117 (Stamatakis, 2006), based on the combined data and 597 taxa and rate smoothed using RELTIME
118 (Tamura et al., 2012) with a single secondary calibration point derived from a wider fossil calibrated
119 analysis of Ericaceae (Schwery et al., 2015). Pirie & al. (2016) identified a "Cape clade" that included
120 all but one of the sampled species of *Erica* found in the CFR. The single exception was *E.*
121 *pauciovulata*, which was placed within a polytomy including the Cape clade and other Afrotemperate
122 lineages. This may, however, be artefactual due to sequence anomalies in the *trnL-trnF-ndhJ* spacer
123 region of *E. pauciovulata*. Preliminary results based on additional sampling including nrDNA ETS (Pirie
124 et al. in prep.) confirm the monophyly of Cape clade including *E. pauciovulata*, and we therefore
125 exclude this taxon from biogeographic analyses to avoid inferring an independent colonisation of the
126 CFR as a result of its uncertain position.

127 *Defining the pure-distance and the niche-based models:* Five biogeographic areas of the *Erica*
128 distribution were defined following Pirie & al. (2016): Europe (including northern Africa); Tropical
129 Africa (TA); Madagascar; Drakensberg; Cape. We obtained occurrence data for *Erica* species from our

own collections, and from PRECIS (representing mostly southern African collections, held by the South African National Biodiversity Institute; http://newposa.sanbi.org/) and GBIF (https://www.gbif.org/) databases. We curated the species occurrence data by removing obviously erroneous locality data, duplicated records, and records with imprecise occurrence data (coordinates with ≤ 3 decimal places, many of which represented centroids of quarter degree squares which were originally represented in PRECIS), but did not further consider the source of or information on the precision of the geographical coordinates, because these are most often not stated in the database-derived occurrence records. This resulted in 6818 individual occurrences representing the species in the phylogenetic trees (Appendix 1). Based on these individual occurrences we estimated the geographic range of the species in the five biogeographic areas (resulting in what we term 'area ranges', i.e. the distributional range of all of the species in a certain biogeographic area) We assessed the area ranges in a biogeographic area placing a buffer of one minutes of arc in radius (ca. 11 km) and 50 m elevation around the individual species occurrences (Europe 4667, Tropical Africa 42, Madagascar 70, Drakensberg 58, and Cape 1981 occurrences; Appendix 2) conservatively aiming at a representative approximation of spatial extent (Nakazato, Warren & Moyle, 2010; Anacker & Strauss, 2014) and ecological conditions of the species' distribution in a respective biogeographic area. These area ranges, which include up to several thousands of spatial points, were used in the subsequent analyses to calculate geographical and ecological distances between biogeographic areas.

To incorporate a measure of geographic proximity among areas in a solely distance-based biogeographic model (the 'geographic distance' model; Fig. 1), we calculated the overall minimum geographic pairwise distances between the area ranges according to Meeus (1999) in WGS84 projection using the raster 2.3-33 package (Hijmans, 2015) in R (R Development Core Team, 2013). We converted geographic distances into dispersal rate multipliers (0-1, whereby the largest distance has the smallest dispersal probability), while comparing the effect of scaling the distances linearly (applying a linear model with intercept of 1 and a slope of -1.52^{-07}) and exponentially (-0.25, -1 and -2).

To incorporate in a niche-based biogeographic model, the 'niche similarity' model (Fig. 1), a measure of climatic similarity between the biogeographic areas we built a multidimensional environmental model representing the full space of all available climates in the global study area (i.e. most of Europe and entire Africa, represented by >0.5 million spatially independently sampled point locations; Appendix 2) using principal component analysis (PCA) in R's ade4 1.6-2 (Dray & Dufour, 2007). We then calculated the pairwise climate similarity between the area ranges (as defined by the species occurrence data; see above) as Schoener's *D* (Schoener, 1968; ranging from 0 = no similarity to 1 = identical) while correcting for the entire climatic variance in the global study area and between the biogeographic areas (Broennimann et al., 2012) by kernel density smoothers using ecospat 2.1.1

165 (Broennimann et al., 2014). Finally, the biogeographic model for the niche similarity hypothesis was
166 defined using the pairwise Schoener's *D* values for the combined PCA axes 1 and 2 directly as
167 dispersal rate multipliers between areas (for details see protocol in Appendix 2).

168 Finally, to consider both geographical and environmental distances in a joint model, also accounting
169 for a negative correlation between both geographic and environmental distances (Kendall's R = -
170 0.64), we used two rate multiplier matrices, representing both climatic niche and physical distance
171 (converted into probabilities; see above), as input.

172 *Biogeographic model testing and ancestral area reconstruction:* We used BioGeoBEARS (Matzke,
173 2013) for parametric model testing, whilst aware of the debate surrounding these models and their
174 comparison (Ree & Sanmartín, 2018; see Results and Discussion). The above defined biogeographic
175 models (Fig. 1) were parameterized using different dispersal rate multipliers (see below and
176 Appendix 3) and compared to null models that do not incorporate any constraints. As input data we
177 used the rate-smoothed ML phylogeny reduced to one tip per sampled species (Pirie & al., 2016; the
178 "best tree"), a file delimiting the distributional range of species, and a file indicating
179 connectivity/distance between the different areas of the *Erica* distribution (varying for the different
180 biogeographic models; Fig. 1, Appendix 3). Model fit of the different nested and non-nested models
181 was tested using the Akaike Information Criterion (AIC) and the delta AIC (Burnham & Anderson,
182 2002). For model testing we additionally used nine trees from the RAxML bootstrap analyses of Pirie
183 & al. (2016) of the same dataset (rate-smoothed using the ape package in R; Paradis & al., 2004).
184 These trees were selected to represent the possible resolutions of phylogenetic uncertainty between
185 the geographically restricted major clades (Appendix 4) but were otherwise chosen randomly with
186 respect to topologies and branch lengths. All hypotheses were implemented with combinations of
187 dispersal-extinction-cladogenesis (DEC; Ree et al., 2005; Ree & Smith, 2008), Bayarea-like or DIVA-
188 like models, with or without allowing long distance dispersal (the "+J" model of Matzke, 2014). We
189 focus on DEC and DEC+J models because these generally fit the data better than Bayarea-like or
190 DIVA-like models.

191 Prior to comparing the different biogeographic hypotheses, we tested whether an unconstrained
192 model fitted the data better than a) restricting the maximum number of areas at nodes to two;
193 and/or b) implementing an adjacent area matrix (Appendix 3; Results). The Southerly stepping stone,
194 Cape to Cairo, and Drakensberg melting pot hypotheses were then run under a range of different
195 dispersal multipliers (0.00, 0.01, 0.05, 0.075, 0.1, 0.25 and 0.5; and for the DEC+J model also on the
196 nine bootstrap trees with dispersal multipliers of 0.01, 0.1, 0.25 and 0.5) to test whether these
197 arbitrary values influenced the results. For niche- and distance-based biogeographic models
198 Schoener's *D* values and geographic distances scaled to probabilities (see above) were used directly

199 as dispersal multipliers (Appendix 3). We also assessed the impact on model fit (given the best fitting
200 model) of a number of different values for the parameter "w", which is an exponent for the dispersal
201 multipliers (which otherwise was fixed to "1"; Appendix 3); and coding of *E. arborea* as European
202 (following Mugrabi de Kuppler et al., 2015), rather than as widespread between Europe and Tropical
203 Africa. Further details and example files for the BioGeoBEARS analyses are presented in Appendix 3.

204 *Estimating dispersal rates*: For the best models under both DEC+J and DEC, given the best tree, we
205 estimated the number and type of biogeographic events across the clade using Biogeographical
206 Stochastic Modelling (BSM) as implemented in BioGeoBEARS (Matzke, 2014). BSM simulates histories
207 of the times and locations of dispersal events. Frequencies were estimated by taking the mean and
208 standard deviation of event counts from 50 BSMs. We also compared the results to that of simple
209 parsimony optimisation using Mesquite v3.31 (Maddison & Maddison, 2006), under the assumption
210 that LDD events are simply rare (Pirie et al., 2012). We incorporated phylogenetic uncertainty by
211 summarising the results over the complete sample of 252 RAxML bootstrap trees adapted from Pirie
212 & al. (2016), and coding *E. arborea* either as widespread between Europe and Tropical Africa or
213 European (Appendix 5).

214

215
216 **Results**

217 *Niche similarity model:* The environmental space that represents all climates available in the study
218 area – most of Europe and all of Africa – and that was used to approximate the climatic similarity
219 between biogeographic areas (area ranges) calculated as hypervolume corrected Schoener's *D*
220 accounting for climatic variation in the study area and between the area ranges, explained >88% of
221 the climate variation on the first two PCA axes. Despite the range of differing conditions within areas,
222 e.g. with rainfall seasonality differing according to elevation, variation between area ranges was
223 considerable (the distribution and the median values for Schoener's *D* per PCA axis pairwise for the
224 areas are presented in Appendix 6, and for the combined axes 1 and 2 in Appendix 7). According to
225 the latter, the Cape and Drakensberg areas are climatically most similar (*D*: 0.71) and Europe and
226 Madagascar are most different (*D*: 0.21). Most similar to the European are the Cape and Drakensberg
227 climates (both *D*: 0.35), and the Tropical Africa climate (*D*: 0.27; Fig. 2C).

228 *Biogeographic model testing:* Assuming that AIC values of the differing models can be compared (but
229 see Ree and Sanmartín, 2018), DEC/DEC+J models generally fit the data better than Bayarea-like or
230 DIVA-like models and DEC+J models generally fit the data better than equivalent DEC ones (Appendix
231 8). Under DEC+J, models including an adjacent area matrix fitted the data better than those without
232 constraint to dispersal. We additionally fixed the maximum number of ancestral areas to two,

233 increasing the speed of the analyses without negatively impacting model fit. Under DEC, models with
234 maximum areas at nodes restricted to two fitted the data better than those without constraint to
235 ancestral ranges. Under both DEC+J and DEC, geographic distance fitted the data better when
236 translated linearly into dispersal rate probabilities (0-1) than when scaled exponentially (Appendix 8);
237 we therefore focus on models using the probabilities, referring to them simply as "geographical
238 distance". The DEC+J results in general do not show the flaws as reported by Ree and Sanmartín
239 (2018). For example, the values for range expansion (parameter d) were similar and low (0.0030 and
240 0.0027 per Ma respectively; Appendix 9). Under DEC+J, cladogenetic dispersal (parameter j) was
241 0.0024 per node, i.e. lower than d (particularly given an average branch length across the *Erica*
242 phylogeny of 1.78 Ma, variance of 11.67) and much lower than the maximum permitted value (3).

243 Under DEC+J given the best tree, the "Drakensberg melting pot", "geographic distance", and
244 "Southerly stepping stone" models revealed the best fit (lowest AIC with deltaAIC ≥2); under DEC the
245 Drakensberg melting pot model alone scored best, but with AIC 141 compared to AIC 131 for DEC+J
246 (Appendix 8). Adopting DEC+J as the generally better fitting and biologically more realistic model (see
247 Discussion), we assessed the results given phylogenetic uncertainty represented by selected
248 bootstrap trees. Based on the bootstrap trees, the combined niche-geographic distance hypothesis
249 was often among the best fitting models (deltaAIC <2 given eight of nine trees), scoring better than
250 pure distance (deltaAIC <2 for five trees), or niche similarity (deltaAIC <2 for four trees) alone. The
251 "Cape to Cairo" model generally fitted better than most other biogeographic scenarios (deltaAIC <2
252 for eight of nine trees, compared to Drakensberg melting pot (deltaAIC <2 for two of nine trees) and
253 southerly stepping stone (not amongst the best fitting models); Table 1; Appendix 8).

254 *Ancestral area reconstruction*: Overall, we infer a colonisation path of *Erica* from Europe to the Cape
255 via an initial migration to Tropical Africa, under DEC+J and irrespective of best fitting model or
256 phylogenetic uncertainty. When *E. arborea* is treated as widespread between Europe and Tropical
257 Africa, the common ancestor of the African/Madagascan clade is inferred to have been similarly
258 widespread. When *E. arborea* is treated as ancestrally European, dispersal from Europe to Tropical
259 Africa is inferred without a transitional widespread distribution. Under DEC, the colonisation path to
260 the Cape is also via an initial migration to Tropical Africa, then a widespread distribution between
261 Tropical Africa and the Cape, followed by an extinction in Tropical Africa. Whether *E. arborea* is
262 treated as widespread between Europe and Tropical Africa or not, the common ancestor of the
263 African/Madagascan clade is inferred to have been similarly widespread between Europe and
264 tropical Africa. Ancestral area reconstructions given the best tree under the best fitting models (as
265 well as under a model without range or dispersal constraints for comparison; in each case under both
266 DEC+J and DEC) are presented in Appendix 13. Overall, ancestral areas inferred under parsimony
267 were consistent with those inferred under parametric models (more so with those under DEC+J,

given that widespread distributions are not incorporated into standard character optimisation), with the numbers and directions of shifts unaffected by phylogenetic uncertainty.

The vast majority of biogeographic events inferred using BSM under both DEC+J and DEC were within-area speciation (97.15 % and 96.26% respectively; Appendix 9). Under DEC+J, few range expansion events were inferred between Europe and Tropical Africa and between Tropical Africa and the Drakensberg region, with most between Cape and the Drakensberg regions (Appendix 10). Dispersal rates between area ranges inferred under BSM are summarised in Fig. 2C. A single founder event (parameter j) was inferred from Tropical Africa to the Cape region, with fewer events between the Drakensberg and Tropical Africa and between Tropical Africa and Madagascar. Overall, most founder events took place from Tropical Africa (1.96 [standard deviation of 0.47] events averaged across 50 BSM; Appendix 11). In addition to the most commonly inferred range expansions given DEC+J, under DEC additional range expansions were inferred from Tropical Africa to Madagascar and from Tropical Africa to the Cape (Appendix 10). With each range expansion under DEC, the corresponding ancestral distribution was widespread. Under both DEC+J and DEC dispersal rates between Tropical Africa and the Drakensberg were roughly symmetrical, as opposed to those between the Cape and the Drakensberg or between Europe and Tropical Africa which were asymmetrical (Fig. 2; Appendix 12).

Discussion

In this study, we modelled shifts between biomes and dispersals over larger distances in the evolution of *Erica*, in order to test six hypotheses for the origins of Afrotemperate plant groups (Fig. 1). Three models concerned general factors considered of importance in limiting plant dispersal: geographical distance, similarity of realised climatic niches, and a combination of geographical and ecological proximity. The remaining three models described specific colonisation hypotheses of the Afrotemperate, in each case proposing a stepwise shift in distributions between adjacent areas. These models differed in the area of origin and in the direction of dispersal: northerly dispersal from the Cape ("Cape to Cairo"), versus southerly dispersal from Europe ("Southerly stepping stone"), or a combination of both (termed here "Drakensberg melting-pot").

Of the stepping-stone-dispersal models, "Cape to Cairo" and/or "Drakensberg melting-pot" fit the data better than "Southerly stepping stone" for all but the best tree, but relative fit of the models was somewhat sensitive to phylogenetic uncertainty (Table 1). By contrast, the positions of areas relative to one another, and the similarities in their realised climatic niche, were consistently prominent in our results. Of the distance models, the combination of geographical and ecological

302 distance fit the data well. Our results showed that these factors are correlated across the *Erica*
303 distribution, but nevertheless given the phylogenetic uncertainty it was the combination of both that
304 often fitted the data better than either of factor individually (or indeed the stepping stone models).
305 The generally better fit of the combined geographic and realised niche model affirms the concerted
306 importance of both factors in shaping distributional patterns of plants (Donoghue 2008; Donoghue
307 and Edwards, 2014). Of the nine range expansion events that we inferred (DEC+J, best tree, best
308 model), seven respectively were between adjacent areas or between areas with similar
309 environmental conditions (where "similar" is arbitrarily defined as a pairwise Schoener's $D > 0.5$; Fig.
310 2). Overall, this represents striking evidence for geographical and ecological distance constraining
311 past and present distributions of *Erica* species, similar to that inferred for other Mediterranean
312 climate plant groups (Skeels & Cardillo, 2017). Irrespective of model fit, the sequence of dispersal
313 events that we inferred from ancestral area reconstructions, based on both the set of best fitting
314 parametric models and a parsimonious interpretation of the infrequent dispersal events (Fig. 2), does
315 resemble a "Drakensberg melting-pot" scenario. The Drakensberg acted as a sink for dispersals from
316 the adjacent Cape and Tropical African regions, but not as a stepping stone (or indeed a
317 "springboard"; Galley & al., 2007).

318 Cape lineages found in the Drakensberg have not dispersed to Tropical Africa, and neither have
319 Tropical Africa lineages found in the Drakensberg dispersed further to the Cape. This is unexpected,
320 not only because of the low distances and high niche similarities involved, but also because of the
321 equivalent events inferred in other similarly distributed plant groups (Galley et al., 2007). Striking in a
322 different way are three unique events: the single dispersals from Europe to Tropical Africa, out of
323 Tropical Africa to the Cape, and out of Tropical Africa to Madagascar, which were each over much
324 longer distances. The dispersals to Tropical Africa and to Madagascar both might have involved shifts
325 in realised niches (indicated by low Schoener's D values of 0.298 and 0.274 respectively); that to the
326 Cape, borderline so (Schoener's D of 0.560; Fig. 2). Notably, the dispersals to tropical Africa and to
327 the Cape coincided with clear increases in diversification rate (Pirie et al., 2016).

328 Potential explanations for these apparent exceptions to the general importance of geographical and
329 ecological distance might be found in the context of the changing climates and geology of the African
330 continent during the timeframe of the *Erica* radiation. The summer-arid climate of the present day
331 Cape has been linked to the establishment of the cold Benguela current off the south-west African
332 coast in the mid Miocene 14-10 Ma (Marlow et al., 2000; Zachos et al., 2001). Evidence from pollen
333 deposited in nearby marine sediments shows an accumulation of typical Cape lineages since roughly
334 the same time, including Ericaceae (Dupont et al., 2011), supported by further evidence from recent
335 dated phylogenies both for the ages of clades in the Cape (e.g. Verboom & al., 2009; Hoffmann & al.,
336 2015) and the origins of fire adapted lineages (Bytebier et al., 2011). The gradual change from a more

337 tropical to a mesic flora and initiation of a regular fire regime in south-western Africa might be
338 ecological changes important for the establishment of *Erica* in the Cape. Whilst the mountains of the
339 Western Cape, home to much of the *Erica*-dominated fynbos vegetation, long predate Miocene
340 climatic changes, the origins of the Drakensberg and Tropical African high mountains, *Erica's* area of
341 first establishments in Africa, are more recent, with uplift in these regions creating montane habitats
342 from the Miocene onwards (McCarthy & Rubidge, 2005).

343 Thus, shifting climates and mountain building created an archipelago of temperate islands across
344 sub-Saharan Africa that were available for colonisation by plants able to tolerate the novel
345 conditions. These included *Erica* species, which had begun to diversify c. 30 Ma in the Northern
346 Hemisphere (Pirie et al., 2016), and which as a clade are characterised by drought resistant leaves
347 (Van Wilgen, Higgins & Bellstedt, 1990) as well as adaptations to post-fire regeneration (Ojeda,
348 1998). However, our analyses of the realised climatic niches of *Erica* species in their different biomes
349 suggests that despite these pre-existing drought and fire adaptations, colonisation of new areas by
350 *Erica* involved further adaptation to rather different climatic conditions, as inferred for tropical alpine
351 *Hypericum* in South America (Nürk, Michling & Linder, 2018) and hypothesised for tropical high
352 alpine plants in general (Gehrke, 2018). In this context, biome shifts and increased diversification
353 rates may be linked: the open field presented by these newly formed, isolated, temperate habitats
354 may have facilitated both the chance establishment of suboptimally adapted plants and their
355 subsequent *in situ* shift into new adaptive zones, promoting accelerated diversification.

356 Neither differences in ecological nor geographic distance present an obvious explanation for why
357 dispersal to the Drakensberg was not followed by further independent colonisations, particularly of
358 the Cape. One possibility could be that within the Drakensberg, Cape and Tropical African elements
359 occupy somewhat differing niches: the former, such as the widespread Cape-Drakensberg species *E.*
360 *cerinthoides* and *E. caffra* predominantly at lower elevations, the latter at higher elevations under
361 conditions differing more to those in the Cape. Another could be niche pre-emption (Silvertown,
362 2004), whereby the single colonisation and rapid species radiation of Cape *Erica* prevented further
363 colonisation by similar competitors.

364 Widespread species such as *E. cerinthoides* and *E. caffra*, found in the Cape and Drakensberg, and *E.*
365 *arborea*, found in Europe and Tropical Africa (Désamoré & al., 2011; Gizaw & al., 2013), are
366 exceptional in *Erica*. Almost all extant species are restricted to just one of the areas as defined here
367 (including species such as *E. silvatica* and *E. benguelensis* that are widespread across disjunct areas
368 within Tropical Africa), and species radiations leading to most of the present day diversity of *Erica*
369 were within single areas (Pirie & al., 2016). This suggests that species distributions were restricted
370 throughout the evolution of the *Erica* African/Madagascan clade, and that the areas remained

371 isolated during this period (i.e. the last c. 15 Ma; Pirie & al., 2016). We would also argue that it lends
372 credibility to results obtained under DEC+J, in which some range shifts were treated as cladogenetic
373 dispersal events (instead of by inferring seemingly implausible widespread distributions), despite
374 arguable drawbacks in the implementation of that model (Ree & Sanmartín, 2018).

375 Nevertheless, the extent and position of suitable habitats across the Afrotemperate shifted
376 considerably during this timeframe, and the implicit assumption of our analyses, that they can be
377 treated as consistent during the *Erica* diversification, is a considerable simplification. This may not
378 impact the results of a broader scale analysis such as the one we present here, but might be
379 important in the context of diversifications within regions, such as those within the Cape (Linder,
380 2003; Dupont et al., 2011; Schnitzler et al., 2012; Hoffmann, Verboom & Cotterill, 2015) or
381 Drakensberg (Bentley, Verboom & Bergh, 2014). To assess the impact of climatic changes on the
382 dramatic radiation of Cape *Erica*, for example, it would be important to translate realised niches into
383 past distributions to model the shifting extents and interconnectedness of populations through time
384 (cf. Mairal & al., 2017).

385 *Conclusions:* The overall picture to be gleaned from the colonisation history of *Erica* across the
386 Afrotemperate is one of infrequent dispersal limited by geographic distance and ecological similarity.
387 Lack of dispersals where they might be expected – in the case of *Erica*, the Drakensberg acting as a
388 sink, rather than stepping stone to wider dispersal – can point to biological and historical
389 idiosyncrasies of particular lineages. Our results also show the importance of single unique events
390 that can run counter to general trends. In *Erica*, three particularly long distance dispersals, two
391 potentially with shifts in the realised niche, were followed by species radiations – most notably in the
392 Cape – that dominate the narrative of the group as a whole. Our results serve to further emphasise
393 the importance of such rare events, in which unique biome shifts fuel dramatic evolutionary
394 radiations.

395

396 Acknowledgements: We thank J. Fagúndez, A. Hitchcock, R. Turner, M. Muasya, C. Stirton, R. Clark, B.
397 Bytebier, M. Pimentel, F. Ojeda, C. Merry, and many others for providing samples and Cape Nature
398 and South Africa National Parks for assistance with permits. We also gratefully acknowledge the
399 computing time granted on the supercomputer Mogon at Johannes Gutenberg University Mainz
400 (www.hpc.uni-mainz.de), and F. Michling for providing R code. Invaluable constructive comments on
401 the previous preprint version of this paper was provided by Andrea Meseguer, Simon Joly, Florian
402 Boucher, and two anonymous reviewers. Funding was provided by the South African National
403 Research Foundation (NRF; DUB and MDP); a postdoctoral fellowship from the Claude Leon
404 Foundation (MDP); DFG (PI1169/1-1, PI1169/1-2, PI1169/2-1 and PI1169/3-1 to MDP); and the

Ministerium für Klimaschutz, Umwelt, Landwirtschaft, Natur- und Verbraucherschutz des Landes Nordrhein-Westfalen, the Faculty of Agriculture Lehr- und Forschungsschwerpunkt „Umweltverträgliche und Standortgerechte Landwirtschaft“, Bonn University; and the Landgard foundation (AMK). Any opinion, finding and conclusion or recommendation expressed in this material is that of the authors and the NRF does not accept liability in this regard.

Author contributions': DUB, MDP & EGHO: conceived the research; NCM, AM, MDP, BG, EGHO & DUB: generated data; MDP, MK & NMN: designed analytical approach; MK: performed BioGeoBEARS analyses; NMN: performed GIS-based environmental analyses; MDP: led the writing (to which all authors contributed).

References

Alsos IG., Eidesen PB., Ehrich D., Skrede I., Westergaard K., Jacobsen GH., Landvik JY., Taberlet P., Brochmann C. 2007. Frequent long-distance plant colonization in the changing Arctic. *Science* 316:1606–9. DOI: 10.1126/science.1139178.

Anacker BL., Strauss SY. 2014. The geography and ecology of plant speciation: range overlap and niche divergence in sister species. *Proceedings of the Royal Society B: Biological Sciences* 281:20132980–20132980. DOI: 10.1098/rspb.2013.2980.

Bellstedt DU., Galley C., Pirie MD., Linder HP. 2012. The Migration of the Palaeotropical Arid Flora: Zygophylloideae as an Example. *Systematic Botany* 37:951–959. DOI: 10.1600/036364412X656608.

Bentley J., Verboom G., Bergh NG. 2014. Erosive processes after tectonic uplift stimulate vicariant and adaptive speciation: evolution in an Afrotemperate-endemic paper daisy genus. *BMC Evolutionary Biology* 14:27. DOI: 10.1186/1471-2148-14-27.

Broennimann O., Fitzpatrick MC., Pearman PB., Petitpierre B., Pellissier L., Yoccoz NG., Thuiller W., Fortin MJ., Randin C., Zimmermann NE., Graham CH., Guisan A. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography* 21:481–497. DOI: 10.1111/j.1466-8238.2011.00698.x.

Broennimann O., Petitpierre B., Randin C., Engler R., Breiner F., D'Amen M., Pellissier L., Pottier J., Pio D., Mateo RG. 2014. ecospat: Spatial ecology miscellaneous methods. *R package version* 1.

Burnham K., Anderson D. 2002. *Model Selection and Multimodel Inference*. New York, Berlin, Heidelberg: Springer Science & Business Media.

Bytebier B., Antonelli A., Bellstedt DU., Linder HP. 2011. Estimating the age of fire in the Cape flora of

438 South Africa from an orchid phylogeny. *Proceedings of the Royal Society B: Biological Sciences*
439 278:188–195. DOI: 10.1098/rspb.2010.1035.
440 Carvajal-Endara S., Hendry AP., Emery NC., Davies TJ. 2017. Habitat filtering not dispersal limitation
441 shapes oceanic island floras: species assembly of the Galápagos archipelago. *Ecology Letters*
442 20:495–504. DOI: 10.1111/ele.12753.
443 Chala D., Zimmermann NE., Brochmann C., Bakkestuen V. 2017. Migration corridors for alpine plants
444 among the 'sky islands' of eastern Africa: do they, or did they exist? *Alpine Botany* 127:133–
445 144. DOI: 10.1007/s00035-017-0184-z.
446 Crisp MD., Arroyo MTK., Cook LG., Gandolfo MA., Jordan GJ., McGlone MS., Weston PH., Westoby
447 M., Wilf P., Linder HP. 2009. Phylogenetic biome conservatism on a global scale. *Nature*
448 458:754–756. DOI: 10.1038/nature07764.
449 Désamoré A., Laenen B., Devos N., Popp M., González-Mancebo JM., Carine MA., Vanderpoorten A.
450 2011. Out of Africa: north-westwards Pleistocene expansions of the heather *Erica arborea*.
451 *Journal of Biogeography* 38:164–176. DOI: 10.1111/j.1365-2699.2010.02387.x.
452 Donoghue MJ. 2008. Colloquium paper: a phylogenetic perspective on the distribution of plant
453 diversity. *Proceedings of the National Academy of Sciences of the United States of America*
454 105:11549–55. DOI: 10.1073/pnas.0801962105.
455 Donoghue MJ., Edwards EJ. 2014. Biome Shifts and Niche Evolution in Plants. *Annual Review of*
456 *Ecology, Evolution, and Systematics* 45:547–572. DOI: 10.1146/annurev-ecolsys-120213-
457 091905.
458 Dray S., Dufour AB. 2007. The ade4 Package: Implementing the Duality Diagram for Ecologists.
459 *Journal of Statistical Software* 22:1–20. DOI: 10.1.1.177.8850.
460 Drummond CS., Eastwood RJ., Miotto STS., Hughes CE. 2012. Multiple Continental Radiations and
461 Correlates of Diversification in Lupinus (Leguminosae): Testing for Key Innovation with
462 Incomplete Taxon Sampling. *Systematic Biology* 61:443–460. DOI: 10.1093/sysbio/syr126.
463 Dupont LM., Linder HP., Rommerskirchen F., Schefuß E. 2011. Climate-driven rampant speciation of
464 the Cape flora. *Journal of Biogeography* 38:1059–1068. DOI: 10.1111/j.1365-
465 2699.2011.02476.x.
466 Fernández-Palacios JM., De Nascimento L., Otto R., Delgado JD., García-Del-Rey E., Arévalo JR.,
467 Whittaker RJ. 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the
468 long-term biogeography of the Atlantic island laurel forests. *Journal of Biogeography* 38:226–
469 246. DOI: 10.1111/j.1365-2699.2010.02427.x.
470 Galbany-Casals M., Unwin M., Garcia-Jacas N., Smissen RD., Susanna A., Bayer RJ. 2014. Phylogenetic
471 relationships in Helichrysum (Compositae: Gnaphalieae) and related genera: Incongruence
472 between nuclear and plastid phylogenies, biogeographic and morphological patterns, and

473 implications for generic delimitation. *Taxon* 63:608–624. DOI: 10.12705/633.8.
474 Galley CC., Bytebier B., Bellstedt DU., Linder HP. 2007. The Cape element in the Afrotemperate flora:
475 from Cape to Cairo? *Proceedings of the Royal Society B: Biological Sciences* 274:535–543. DOI:
476 10.1098/rspb.2006.0046.
477 García-Aloy S., Vitales D., Roquet C., Sanmartín I., Vargas P., Molero J., Kamau P., Aldasoro JJ.,
478 Alarcón M. 2017. North-west Africa as a source and refuge area of plant biodiversity: a case
479 study on Campanula kremeri and Campanula occidentalis. *Journal of Biogeography* 44:2057–
480 2068. DOI: 10.1111/jbi.12997.
481 Gehrke B. 2018. Staying cool: preadaptation to temperate climates required for colonising tropical
482 alpine-like environments. *PhytoKeys* in press:111. DOI: 10.3897/phytokeys.96.13353.
483 Gehrke B., Linder HP. 2009. The scramble for Africa: pan-temperate elements on the African high
484 mountains. *Proceedings of the Royal Society B: Biological Sciences* 276:2657–2665. DOI:
485 10.1098/rspb.2009.0334.
486 Gizaw A., Brochmann C., Nemomissa S., Wondimu T., Masao CA., Tusiime FM., Abdi AA., Oxelman B.,
487 Popp M., Dimitrov D. 2016. Colonization and diversification in the African 'sky islands': insights
488 from fossil-calibrated molecular dating of *Lychnis* (Caryophyllaceae). *New Phytologist* 211:719–
489 734. DOI: 10.1111/nph.13937.
490 Gizaw A., Kebede M., Nemomissa S., Ehrich D., Bekele B., Mirré V., Popp M., Brochmann C. 2013.
491 Phylogeography of the heathers *Erica arborea* and *E. trimera* in the afro-alpine 'sky islands'
492 inferred from AFLPs and plastid DNA sequences. *Flora - Morphology, Distribution, Functional*
493 *Ecology of Plants* 208:453–463. DOI: 10.1016/j.flora.2013.07.007.
494 Higgins SI., Richardson DM. 1999. Predicting Plant Migration Rates in a Changing World: The Role of
495 Long-Distance Dispersal. *The American Naturalist* 153:464–475. DOI: 10.1086/303193.
496 Hijmans RJ. 2015. raster: Geographic data analysis and modeling. [R package].
497 Hoffmann V., Verboom GA., Cotterill FPD. 2015. Dated Plant Phylogenies Resolve Neogene Climate
498 and Landscape Evolution in the Cape Floristic Region. *PLOS ONE* 10:e0137847. DOI:
499 10.1371/journal.pone.0137847.
500 Jordano P. 2017. What is long-distance dispersal? And a taxonomy of dispersal events. *Journal of*
501 *Ecology* 105:75–84. DOI: 10.1111/1365-2745.12690.
502 Kadereit JW., Baldwin BG. 2012. Western Eurasian-western North American disjunct plant taxa: The
503 dry-adapted ends of formerly widespread North temperate mesic lineages-and examples of
504 long-distance dispersal. *Taxon* 61:3–17.
505 Kim SC., McGowen MR., Lubinsky P., Barber JC., Mort ME., Santos-Guerra A. 2008. Timing and tempo
506 of early and successive adaptive radiations in Macaronesia. *PLoS ONE* 3:1–7. DOI:
507 10.1371/journal.pone.0002139.

508 Knox EB., Palmer JD. 1998. Chloroplast DNA evidence on the origin and radiation of the giant lobelias
509 in eastern Africa. *Systematic Botany* 23:109–149.
510 Kowalski R., Fagúndez J. 2017. *Maiella miocaenica* gen. et sp. nov., a New Heather Genus (Ericeae,
511 Ericaceae) from the Central European Miocene. *International Journal of Plant Sciences* 178:411–
512 420. DOI: 10.1086/691461.
513 Linder HP. 2003. The radiation of the Cape flora, southern Africa. *Biological Reviews* 78:597–638.
514 DOI: Doi 10.1017/S1464793103006171.
515 Linder HP., Antonelli A., Humphreys AM., Pirie MD., Wüest RO. 2013. What determines
516 biogeographical ranges? Historical wanderings and ecological constraints in the danthonioid
517 grasses. *Journal of Biogeography* 40:821–834. DOI: 10.1111/jbi.12070.
518 Maddison WP., Maddison DR. 2006. Mesquite: a modular system for evolutionary analysis.
519 Mairal M., Sanmartín I., Pellissier L. 2017. Lineage-specific climatic niche drives the tempo of
520 vicariance in the Rand Flora. *Journal of Biogeography* 44:911–923. DOI: 10.1111/jbi.12930.
521 Marlow JR., Lange CB., Wefer G., Rosell-Mele A. 2000. Upwelling intensification as part of the
522 Pliocene-Pleistocene climate transition. *Science* 290:2288. DOI: 10.1126/science.290.5500.2288.
523 Matzke NJ. 2013. Probabilistic Historical Biogeography: New Models for Founder-Event Speciation,
524 Imperfect Detection, and Fossils Allow Improved Accuracy and Model- Testing. University of
525 California, Berkeley.
526 Matzke NJ. 2014. Model Selection in Historical Biogeography Reveals that Founder-Event Speciation
527 Is a Crucial Process in Island Clades. *Systematic Biology* 63:951–970. DOI:
528 10.1093/sysbio/syu056.
529 McCarthy T., Rubidge B. 2005. *The story of earth & life: a southern African perspective on a 4.6*
530 *billion-year journey*. Cape Town: Struik Publishers.
531 McGuire AF., Kron KA. 2005. Phylogenetic relationships of European and African ericas. *International*
532 *Journal of Plant Sciences* 166:311–318. DOI: 10.1086/427478.
533 Meeus J. 1999. *Astronomical algorithms.* Willman-Bell.
534 Merckx VSFT., Hendriks KP., Beentjes KK., Mennes CB., Becking LE., Peijnenburg KTCA., Afendy A.,
535 Arumugam N., De Boer H., Biun A., Buang MM., Chen PP., Chung AYC., Dow R., Feijen FAA.,
536 Feijen H., Soest CF Van., Geml J., Geurts R., Gravendeel B., Hovenkamp P., Imbun P., Ipor I.,
537 Janssens SB., Jocqué M., Kappes H., Khoo E., Koomen P., Lens F., Majapun RJ., Morgado LN.,
538 Neupane S., Nieser N., Pereira JT., Rahman H., Sabran S., Sawang A., Schwallier RM., Shim PS.,
539 Smit H., Sol N., Spait M., Stech M., Stokvis F., Sugau JB., Suleiman M., Sumail S., Thomas DC.,
540 Van Tol J., Tuh FYY., Yahya BE., Nais J., Repin R., Lakim M., Schilthuizen M. 2015. Evolution of
541 endemism on a young tropical mountain. *Nature* 524:347–350. DOI: 10.1038/nature14949.
542 Míguez M., Gehrke B., Maguilla E., Jiménez-Mejías P., Martín-Bravo S. 2017. Carex sect.

543 Rhynchocystis (Cyperaceae): a Miocene subtropical relict in the Western Palaearctic showing a
544 dispersal-derived Rand Flora pattern. *Journal of Biogeography* 44:2211–2224. DOI:
545 10.1111/jbi.13027.
546 Mugrabi de Kuppler AL., Fagúndez J., Bellstedt DU., Oliver EGH., Léon J., Pirie MD. 2015. Testing
547 reticulate versus coalescent origins of *Erica lusitanica* using a species phylogeny of the northern
548 heathers (Ericeae, Ericaceae). *Molecular Phylogenetics and Evolution* 88:121–131. DOI:
549 10.1016/j.ympev.2015.04.005.
550 Muñoz J., Felicísimo AM., Cabezas F., Burgaz AR., Martínez ILB-4319. 2004. Wind as a long-distance
551 dispersal vehicle in the Southern Hemisphere. *Science* 304:1144–1147.
552 Nakazato T., Warren DL., Moyle LC. 2010. Ecological and geographic modes of species divergence in
553 wild tomatoes. *American Journal of Botany* 97:680–693. DOI: 10.3732/ajb.0900216.
554 Nathan R. 2006. Long-Distance Dispersal of Plants. *Science* 313:786–788. DOI:
555 10.1126/science.1124975.
556 Nürk NM., Michling F., Linder HP. 2018. Are the radiations of temperate lineages in tropical alpine
557 ecosystems pre-adapted? *Global Ecology and Biogeography* 27:334–345. DOI:
558 10.1111/geb.12699.
559 Nürk NM., Uribe-Convers S., Gehrke B., Tank DC., Blattner FR. 2015. Oligocene niche shift, Miocene
560 diversification - cold tolerance and accelerated speciation rates in the St. John's Worts
561 (Hypericum, Hypericaceae). *BMC evolutionary biology* 15:80. DOI: 10.1186/s12862-015-0359-4.
562 Ojeda F. 1998. Biogeography of seeder and resprouter Erica species in the Cape Floristic Region—
563 Where are the resprouters? *Biological Journal of the Linnean Society* 63:331–347. DOI:
564 10.1111/j.1095-8312.1998.tb01521.x.
565 Oliver EGH. 2012. Ericaceae. In: Manning JC, Goldblatt P eds. *Plants of the Greater Cape Floristic*
566 *Region, Volume 1: The Core Cape Flora*. Strelitzia. Pretoria: South African National Biodiversity
567 Institute (SANBI Publishing), 482—511.
568 Paradis E., Claude J., Strimmer K. 2004. APE: Analyses of Phylogenetics and Evolution in R language.
569 *Bioinformatics* 20:289–290. DOI: 10.1093/bioinformatics/btg412.
570 Pirie MD., Humphreys AM., Antonelli A., Galley C., Linder HP. 2012. Model uncertainty in ancestral
571 area reconstruction: A parsimonious solution? *Taxon* 61:652–664. DOI: 10.5167/uzh-64515.
572 Pirie MD., Oliver EGH., Bellstedt DU. 2011. A densely sampled ITS phylogeny of the Cape flagship
573 genus Erica L. suggests numerous shifts in floral macro-morphology. *Molecular Phylogenetics*
574 *and Evolution* 61:593–601. DOI: 10.1016/j.ympev.2011.06.007.
575 Pirie MD., Oliver EGH., Mugrabi de Kuppler A., Gehrke B., Le Maitre NC., Kandziora M., Bellstedt DU.
576 2016. The biodiversity hotspot as evolutionary hot-bed: spectacular radiation of Erica in the
577 Cape Floristic Region. *BMC Evolutionary Biology* 16:190. DOI: 10.1186/s12862-016-0764-3.

578 Pokorny L., Riina R., Mairal M., Meseguer AS., Culshaw V., Cendoya J., Serrano M., Carbajal R., Ortiz
579 S., Heuertz M., Sanmartín I. 2015. Living on the edge: timing of Rand Flora disjunctions
580 congruent with ongoing aridification in Africa. *Frontiers in Genetics* 6:154. DOI:
581 10.3389/fgene.2015.00154.
582 R Development Core Team. 2013. R: A language and environment for statistical computing.
583 Ree RH., Moore BR., Webb CO., Donoghue MJ. 2005. A likelihood framework for inferring the
584 evolution of geographic range on phylogenetic trees. *Evolution; international journal of organic*
585 *evolution* 59:2299–2311. DOI: 10.1554/05-172.1.
586 Ree RH., Sanmartín I. 2018. Conceptual and statistical problems with the DEC+J model of founder-
587 event speciation and its comparison with DEC via model selection. *Journal of Biogeography*.
588 DOI: 10.1111/jbi.13173.
589 Ree RH., Smith SA. 2008. Maximum likelihood inference of geographic range evolution by dispersal,
590 local extinction, and cladogenesis. *Systematic biology* 57:4–14. DOI:
591 10.1080/10635150701883881.
592 Ruhfel BR., Bove CP., Philbrick CT., Davis CC. 2016. Dispersal largely explains the gondwanan
593 distribution of the ancient tropical clusioid plant clade. *American Journal of Botany* 103:1117–
594 1128. DOI: 10.3732/ajb.1500537.
595 Sanmartín I., Anderson CL., Alarcon M., Ronquist F., Aldasoro JJ. 2010. Bayesian island biogeography
596 in a continental setting: the Rand Flora case. *Biology Letters* 6:703–707. DOI:
597 10.1098/rsbl.2010.0095.
598 Schnitzler J., Graham CH., Dormann CF., Schiffers K., Peter Linder H. 2012. Climatic niche evolution
599 and species diversification in the Cape flora, South Africa. *Journal of Biogeography* 39:2201–
600 2211. DOI: 10.1111/jbi.12028.
601 Schoener TW. 1968. The Anolis Lizards of Bimini: Resource Partitioning in a Complex Fauna. *Ecology*
602 49:704–726. DOI: 10.2307/1935534.
603 Schwery O., Onstein RE., Bouchenak-Khelladi Y., Xing Y., Carter RJ., Linder HP. 2015. As old as the
604 mountains: The radiations of the Ericaceae. *New Phytologist* 207:355–367. DOI:
605 10.1111/nph.13234.
606 Silvertown J. 2004. The Ghost of Competition Past in the Phylogeny of Island Endemic Plants. *J. Ecol.*
607 92:168–173. DOI: 10.1111/j.1365-2745.2004.00853.x.
608 Skeels A., Cardillo M. 2017. Environmental niche conservatism explains the accumulation of species
609 richness in Mediterranean-hotspot plant genera. *Evolution*:582–594. DOI: 10.1111/evo.13179.
610 Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with
611 thousands of taxa and mixed models. *Bioinformatics* 22:2688–2690. DOI:
612 10.1093/bioinformatics/btl446.

613 Tamura K., Battistuzzi FU., Billing-Ross P., Murillo O., Filipski A., Kumar S. 2012. Estimating divergence
614 times in large molecular phylogenies. *Proceedings of the National Academy of Sciences of the*
615 *United States of America* 109:19333–19338. DOI: 10.1073/pnas.1213199109.
616 Uribe-Convers S., Tank DC. 2015. Shifts in diversification rates linked to biogeographic movement
617 into new areas: An example of a recent radiation in the Andes. *American Journal of Botany*
618 102:1854–1869. DOI: 10.3732/ajb.1500229.
619 Verboom GA., Archibald JK., Bakker FT., Bellstedt DU., Conrad F., Dreyer LL., Forest FF., Galley CC.,
620 Goldblatt P., Henning JF., Mummenhoff K., Linder HP., Muasya AM., Oberlander KC., Savolainen
621 V., Snijman DA., Niet T van der T van der., Nowell TL. 2009. Origin and diversification of the
622 Greater Cape flora: Ancient species repository, hot-bed of recent radiation, or both? *Molecular*
623 *Phylogenetics and Evolution* 51:44–53. DOI: 10.1016/j.ympev.2008.01.037.
624 Verdcourt B. 1969. The arid corridor between the North-East and South-West areas of Africa. In: van
625 Zinderen Bakker EM ed. *Paleoecology of Africa*. Cape Town: Balkema, 140–144.
626 Viana DS., Gangoso L., Bouten W., Figuerola J. 2015. Overseas seed dispersal by migratory birds.
627 *Proceedings of the Royal Society B: Biological Sciences* 283:20152406. DOI:
628 dx.doi.org/10.1098/rspb.2015.2406.
629 White F. 1981. The history of the Afromontane archipelago and the scientific need for its
630 conservation. *African Journal of Ecology* 19:33–54. DOI: 10.1111/j.1365-2028.1981.tb00651.x.
631 White F. 1983. The vegetation of Africa: a descriptive memoir to accompany the
632 UNESCO/AETFAT/UNSO vegetation map of Africa. *Natural Resources Research* 20:1–356.
633 Van Wilgen BW., Higgins KB., Bellstedt DU. 1990. The role of vegetation structure and fuel chemistry
634 in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *The*
635 *Journal of Ecology* 78:210–222. DOI: 10.2307/2261046.
636 Zachos J., Pagani M., Sloan L., Thomas E., Billups K. 2001. Trends, rhythms, and aberrations in global
637 climate 65 Ma to present. *Science* 292:686–693. DOI: 10.1126/science.1059412.
638

Figures

Fig. 1: Biogeographic hypotheses. The pure geographic distance model; niche similarity, implying colonisation of areas with the most similar climatic niche (Donoghue 2008); these together constituting a combined geographic and niche similarity model; stepping stone: stepwise southerly colonisation of the Afrotemperate from Europe (following McGuire and Kron, 2005); Cape to Cairo: stepwise northerly colonisation of the Afrotemperate from the Cape (following Galley et al., 2007); necessarily preceded by LDD from Europe; and Drakensberg melting pot: the Drakensberg colonised by both southerly and northerly stepwise dispersal.

Fig. 2: Biogeographic scenario. A) Inferred dispersal scenario between the biogeographic areas (colour coded "area ranges" as assessed by the buffered species occurrence data) depicted on the global study area. **B**) The phylogeny of *Erica* with a representation of ancestral areas derived from a single BSM analysis using the best tree and model (under DEC+J). **C**) Climate similarity between area ranges given as hypervolume corrected pairwise climate similarity (Schoener's D; with $D \geq 0.5$ in dark grey, and $D < 0.5$ in light grey; Table S8) with superimposed black arrows scaled to the dispersal rates per Ma inferred between areas (Table S13). Ma, million years.

Tables

Table 1: Best fitting biogeographic models given the best tree (DEC+J and DEC) and nine selected bootstrap trees (DEC+J). Dispersal multipliers are indicated where relevant, as are the Log likelihood (LnL), Akaike Information Criterion (AIC), and overall deltaAIC scores for models. Models with deltaAIC of 0 are indicated in bold type. DMP=Drakensberg mekting-pot; Dist=Distance; SSS=Southerly stepping-stone; CtoC=Cape to Cairo

Tree	**Model**	Dispersal multiplier	LnL	AIC	deltaAIC
Best (DEC+J)	**DMP**	**0.5**	**-62.5**	**131**	**0**
	DMP	**0.1**	**-62.5**	**131**	**0**
	DMP	**0.25**	**-62.5**	**131**	**0**
	DMP	0.75	-62.6	131.2	0.2
	Dist	-	-62.8	131.6	0.58
	SSS	0.5	-63.1	132.3	1.3
	SSS	0.25	-63.3	132.7	1.7
Best (DEC)	**DMP**	**0.75**	**-68.6**	**141.2**	**0**
	DMP	0.5	-68.7	141.3	0.1
BS 0_0	**Niche+Dist**	**-**	**-61.2**	**128.4**	**0**
	CtoC	0.25	-61.7	129.4	1
	CtoC	0.1	-62.1	130.1	1.7
	Dist	-	-62.2	130.4	2
0_1	**Niche+Dist**	**-**	**-65.6**	**137.1**	**0**
	CtoC	0.1	-65.8	137.6	0.5
	CtoC	0.25	-66.1	138.3	1.2
0_2	**Niche+Dist**	**-**	**-60.2**	**126.3**	**0**
	CtoC	0.25	-60.4	126.7	0.4
	CtoC	0.1	-60.4	126.9	0.6
	Dist	-	-61	127.9	1.6
1_0	**CtoC**	**0.1**	**-58.7**	**123.5**	**0**
	CtoC	0.25	-59.5	124.9	1.4
1_1	**Niche+Dist**	**-**	**-61.7**	**129.4**	**0**
	Niche	-	-62.6	131.2	1.8
1_2	**Niche+Dist**	**-**	**-55.9**	**117.9**	**0**
	CtoC	0.25	-56.5	119	1.1
	CtoC	0.1	-56.9	119.7	1.8
	Dist	-	-56.9	119.7	1.8
2_0	**Niche+Dist**	**-**	**-62.3**	**130.6**	**0**
	CtoC	0.25	-62.6	131.2	0.6
	Dist	-	-62.8	131.5	0.9

	CtoC	0.1	-62.9	131.8	1.2
	CtoC	0.5	-63.1	132.3	1.7
	Niche	-	-63.2	132.4	1.8
2_1	**Dist**	**-**	**-56.5**	**119.1**	**0**
	DMP	0.1	-56.6	119.2	0.1
	DMP	0.25	-56.6	119.2	0.1
	DMP	0.5	-57	120	0.9
	CtoC	0.5	-57.2	120.4	1.3
	Niche+Dist	-	-57.2	120.4	1.3
	CtoC	0.25	-57.5	121	1.9
	Niche	-	-57.6	121.1	2
2_2	**Dist**	**-**	**-65.3**	**135.6**	**0**
	Niche+Dist	-	-65.2	136.4	0.8
	DMP	0.25	-65.5	137	1.4
	CtoC	0.5	-65.5	137	1.4
	DMP	0.1	-65.5	137.1	1.5
	CtoC	0.25	-65.6	137.1	1.5
	Niche	-	-65.8	137.5	1.9
	DMP	0.5	-65.8	137.6	2

664 **Appendices**

665 **Appendix 1: Methods: occurrence data**

666 **Appendix 2: Methods: Global environmental space, area ranges, and climate similarity analysis**

667 **Appendix 3: Methods: Biogeographic models; example files for BioGeoBEARS analyses**

668 **Appendix 4: Methods: Selected bootstrap trees used to represent phylogenetic uncertainty**
669 **between geographically restricted major clades**

670 **Appendix 5: Methods: Mesquite file used for parsimony ancestral state reconstruction including**
671 **RAXML bootstrap trees**

672 **Appendix 6: Results: pairwise climate similarity (Schoener's *D*) between biogeographic areas per PC**
673 **axis**

674 **Appendix 7: Results: Pairwise climate similarity (Schoener's *D*) between biogeographic areas for**
675 **combined PC axes**

676 **Appendix 8: Results of the different models under DEC+J and DEC (generally the better models**
677 **compared to DIVA-like and BAYAREA-like-models)**

678 **Appendix 9: Results: Summary of event counts from 50 biogeographical stochastic mappings under**
679 **the best inferred model using the best tree**

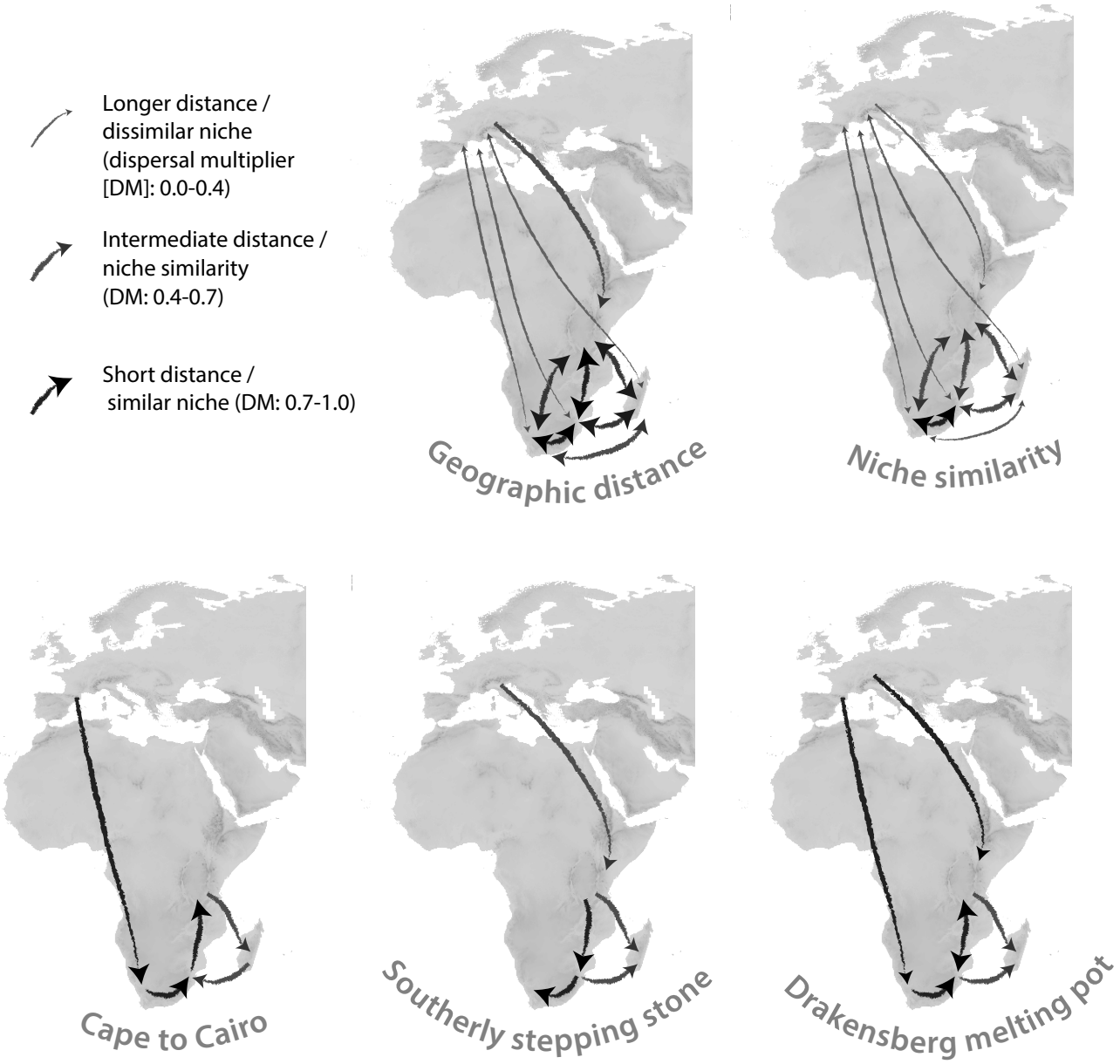
680 **Appendix 10: Results: Number of range-expansion dispersal events (mean and standard deviation**
681 **of all observed "d" dispersals) averaged across 50 biogeographical stochastic mappings under the**
682 **best inferred model using the best tree.**

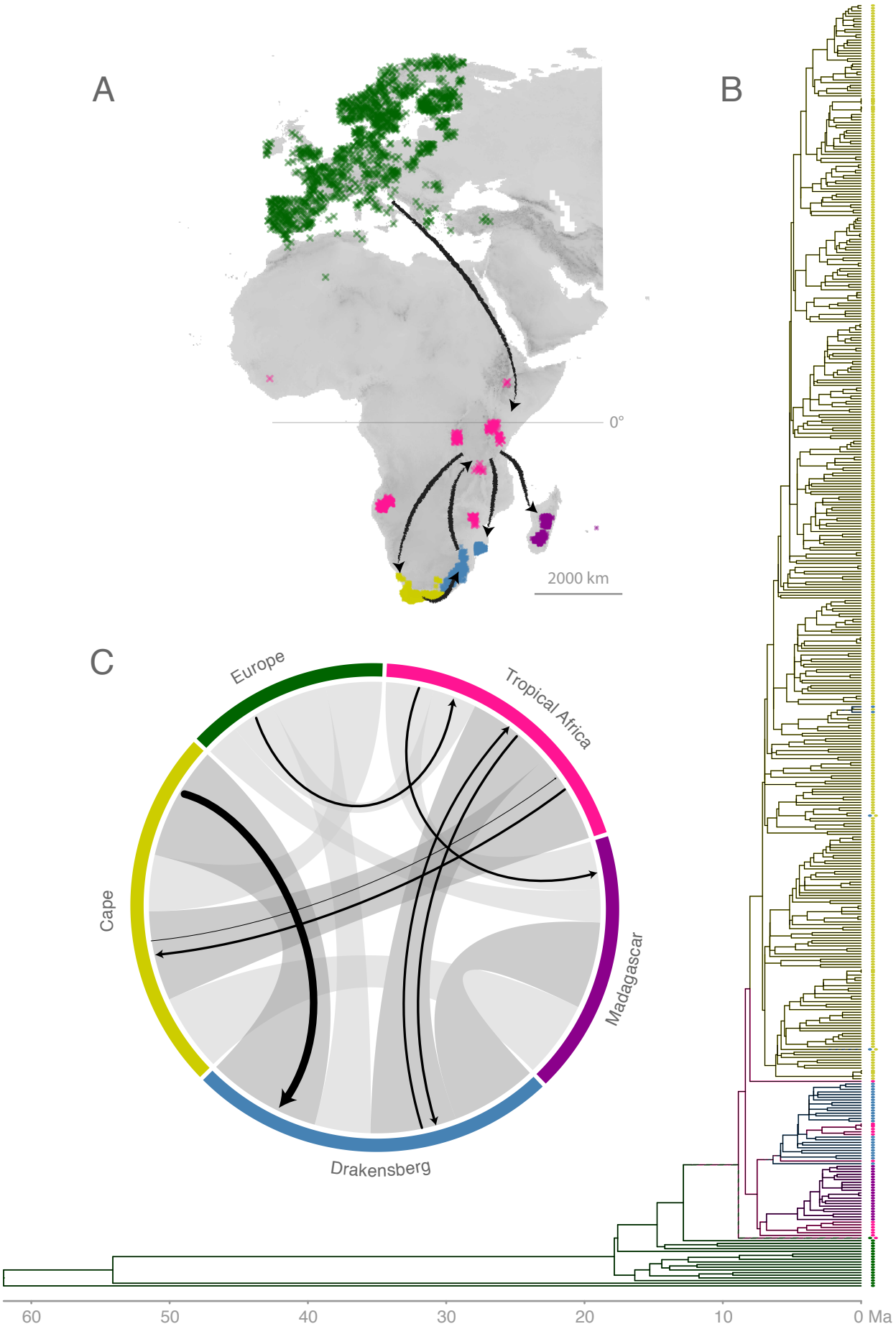
683 **Appendix 11: Results: Number of cladogenetic dispersal events (mean and standard deviation of all**
684 **observed jump 'j' dispersals) averaged from 50 biogeographical stochastic mappings under the best**
685 **inferred model using the best tree.**

686 **Appendix 12: Results: Number of all dispersal events (mean and standard deviation of all observed**
687 **anagenetic 'a', 'd' dispersals, PLUS cladogenetic founder/jump dispersal) averaged from 50**
688 **biogeographical stochastic mappings under the best inferred model using the best tree.**

689 **Appendix 13: Results: Ancestral area reconstructions inferred using BioGeoBEARS given the best**
690 **tree under the best fitting model given A: DEC+J; B: DEC; and without range or dispersal constraint:**
691 **C: DEC+J; D: DEC. For each model the single most probable state is shown first (boxes with areas at**
692 **nodes) followed by the relative probability of each state represented with pie charts at nodes.**
693 **Areas are represented by colours: Dark blue for Europe (E); green for Tropical Africa (T); yellow for**

Madagascar (M); light blue for Drakensberg (D); red for Cape (C); and further colours for widespread distributions as indicated in the legends.


Longer distance / dissimilar niche (dispersal multiplier [DM]: 0.0-0.4)
Intermediate distance / niche similarity (DM: 0.4-0.7)
Short distance / similar niche (DM: 0.7-1.0)
Geographic distance
Niche similarity
Cape to Cairo
Southerly stepping stone
Drakensberg melting pot


A
0°
2000 km
B
C
Europe
Tropical Africa
Madagascar
Drakensberg
Cape
60
50
40
30
20
10
0 Ma