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

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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

Mediterranean climates of southern Europe and the Cape to colder climes of northern Europe and the non-seasonal temperate habitats of the high mountains in Tropical Africa. These habitats are also separated by considerable geographic distances, isolated by expanses of inhospitable ecosystems and/or ocean. Nonetheless, similar distribution patterns across Europe and Africa are observed in different plant groups (e.g. Gizaw et al., 2016; Mairal, Sanmartín & Pellissier, 2017).

Organisms adapted to different habitats respond differently to changing environmental conditions (Mairal, Sanmartín & Pellissier, 2017; Chala et al., 2017). Distribution patterns of arid-adapted plant groups, for which suitable habitats in Africa have been more contiguously distributed (Bellstedt et al., 2012), might thus be best described by biogeographic scenarios emphasising vicariance processes, such as for example the "Rand Flora" representing plant lineages that show similar disjunct distributions around the continental margins of Africa (Sanmartín et al., 2010; Pokorny et al., 2015), or the "African arid corridor" hypothesis that seeks to explain disjunct distributions between the Horn of Africa and arid south-western Africa (Verdcourt, 1969; White, 1983). Models that invoke concerted patterns of LDD might instead apply to plants adapted to habitats that remained largely isolated over time (Knox & Palmer, 1998; Galbany-Casals et al., 2014; Nürk et al., 2015; Míguez et al., 2017). Examples include the shared arid adapted elements of Macronesia and adjacent North-West Africa and Mediterranean (Kim et al., 2008; Fernández-Palacios et al., 2011; García-Aloy et al., 2017), and the more mesic temperate or tropical alpine habitats of the "sky islands" of East Africa, in which, for example, multiple lineages originated from northern temperate environments (Gehrke & Linder, 2009; Gizaw et al., 2013, 2016).

A more specific biogeographic scenario, inferred from Cape clades with distributions very similar to that of *Erica,* involves dispersal north from the Cape to the East African mountains via the Drakensberg ("Cape to Cairo"; Galley & al., 2007). McGuire & Kron (2005) proposed a different scenario for *Erica* instead: southerly stepping stone dispersal through the African high mountains to the Cape. Both scenarios, however, imply that dispersal is more frequent between adjacent areas/over shorter distances. Short distance or stepping stone dispersal may indeed be more probable than LDD (Nathan, 2006), and distance alone could conceivably be more important than directionality (Linder et al., 2013). On the other hand, the probabilities of LDDs are hard to model (Higgins & Richardson, 1999; Nathan, 2006), in part because (observable) LDD events also involve successful establishment in more or less distinct environments (Donoghue & Edwards, 2014). Thus geographic distance and ecological suitability might individually constrain the biogeographic history of plants, or the interplay between both factors may be decisive (Donoghue, 2008; Carvajal-Endara et al., 2017), so much so that clades with similar ecological tolerances and origin might show convergence to similar distribution patterns (Merckx et al., 2015; Gizaw et al., 2016; Mairal, Sanmartín & Pellissier, 2017).

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

107

108 **Materials and Methods**

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

126 *Defining the pure-distance and the niche-based models:* Five biogeographic areas of the *Erica*
127 distribution were defined following Pirie & al. (2016): Europe (including northern Africa); Tropical
128 Africa (TA); Madagascar; Drakensberg; Cape. We obtained occurrence data for *Erica* species from our
129 own collections, and from PRECIS (representing mostly southern African collections, held by the
130 South African National Biodiversity Institute; http://newposa.sanbi.org/) and GBIF
131 (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 (Broennimann et al., 2014). Finally, the biogeographic model for the niche similarity hypothesis was defined using the pairwise Schoener's *D* values for the combined PCA axes 1 and 2 directly as dispersal rate multipliers between areas (for details see protocol in Appendix 2).

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

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

190 Prior to comparing the different biogeographic hypotheses, we tested whether an unconstrained
191 model fitted the data better than a) restricting the maximum number of areas at nodes to two;
192 and/or b) implementing an adjacent area matrix (Appendix 3; Results). The Southerly stepping stone,
193 Cape to Cairo, and Drakensberg melting pot hypotheses were then run under a range of different
194 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
195 nine bootstrap trees with dispersal multipliers of 0.01, 0.1, 0.25 and 0.5) to test whether these
196 arbitrary values influenced the results. For niche- and distance-based biogeographic models
197 Schoener's *D* values and geographic distances scaled to probabilities (see above) were used directly
198 as dispersal multipliers (Appendix 3). We also assessed the impact on model fit (given the best fitting
199 model) of a number of different values for the parameter "w", which is an exponent for the dispersal
200 multipliers (which otherwise was fixed to "1"; Appendix 3); and coding of *E. arborea* as European

201 (following Mugrabi de Kuppler et al., 2015), rather than as widespread between Europe and Tropical
202 Africa. Further details and example files for the BioGeoBEARS analyses are presented in Appendix 3.

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

213

214
215 **Results**

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

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

235 translated linearly into dispersal rate probabilities (0-1) than when scaled exponentially (Appendix 8);
236 we therefore focus on models using the probabilities, referring to them simply as "geographical
237 distance". The DEC+J results in general do not show the flaws as reported by Ree and Sanmartín
238 (2018). For example, the values for range expansion (parameter d) were similar and low (0.0030 and
239 0.0027 per Ma respectively; Appendix 9). Under DEC+J, cladogenetic dispersal (parameter j) was
240 0.0024 per node, i.e. lower than d (particularly given an average branch length across the *Erica*
241 phylogeny of 1.78 Ma, variance of 11.67) and much lower than the maximum permitted value (3).

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

253 *Ancestral area reconstruction*: Overall, we infer a colonisation path of *Erica* from Europe to the Cape
254 via an initial migration to Tropical Africa, under DEC+J and irrespective of best fitting model or
255 phylogenetic uncertainty. When *E. arborea* is treated as widespread between Europe and Tropical
256 Africa, the common ancestor of the African/Madagascan clade is inferred to have been similarly
257 widespread. When *E. arborea* is treated as ancestrally European, dispersal from Europe to Tropical
258 Africa is inferred without a transitional widespread distribution. Under DEC, the colonisation path to
259 the Cape is also via an initial migration to Tropical Africa, then a widespread distribution between
260 Tropical Africa and the Cape, followed by an extinction in Tropical Africa. Whether *E. arborea* is
261 treated as widespread between Europe and Tropical Africa or not, the common ancestor of the
262 African/Madagascan clade is inferred to have been similarly widespread between Europe and
263 tropical Africa. Ancestral area reconstructions given the best tree under the best fitting models (as
264 well as under a model without range or dispersal constraints for comparison; in each case under both
265 DEC+J and DEC) are presented in Appendix 13. Overall, ancestral areas inferred under parsimony
266 were consistent with those inferred under parametric models (more so with those under DEC+J,
267 given that widespread distributions are not incorporated into standard character optimisation), with
268 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 distance fit the data well, and given the phylogenetic uncertainty, often better than either of these factors individually or the stepping stone models. The generally better fit of the combined geographic and realised niche model affirms the concerted importance of both factors in shaping distributional

304 patterns of plants (Donoghue 2008; Donoghue and Edwards, 2014). Of the nine range expansion
305 events that we inferred (DEC+J, best tree, best model), seven respectively were between adjacent
306 areas or between areas with similar environmental conditions (where "similar" is arbitrarily defined
307 as a pairwise Schoener's *D* > 0.5; Fig. 2). Overall, this represents striking evidence for geographical
308 and ecological distance constraining past and present distributions of *Erica* species, similar to that
309 inferred for other Mediterranean climate plant groups (Skeels & Cardillo, 2017). Irrespective of
310 model fit, the sequence of dispersal events that we inferred from ancestral area reconstructions,
311 based on both the set of best fitting parametric models and a parsimonious interpretation of the
312 infrequent dispersal events (Fig. 2), does resemble a "Drakensberg melting-pot" scenario. The
313 Drakensberg acted as a sink for dispersals from the adjacent Cape and Tropical African regions, but
314 not as a stepping stone (or indeed a "springboard"; Galley & al., 2007).

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

325 Potential explanations for these apparent exceptions to the general importance of geographical and
326 ecological distance might be found in the context of the changing climates and geology of the African
327 continent during the timeframe of the *Erica* radiation. The summer-arid climate of the present day
328 Cape has been linked to the establishment of the cold Benguela current off the south-west African
329 coast in the mid Miocene 14-10 Ma (Marlow et al., 2000; Zachos et al., 2001). Evidence from pollen
330 deposited in nearby marine sediments shows an accumulation of typical Cape lineages since roughly
331 the same time, including Ericaceae (Dupont et al., 2011), supported by further evidence from recent
332 dated phylogenies both for the ages of clades in the Cape (e.g. Verboom & al., 2009; Hoffmann & al.,
333 2015) and the origins of fire adapted lineages (Bytebier et al., 2011). The gradual change from a more
334 tropical to a mesic flora and initiation of a regular fire regime in south-western Africa might be
335 ecological changes important for the establishment of *Erica* in the Cape. Whilst the mountains of the
336 Western Cape, home to much of the *Erica*-dominated fynbos vegetation, long predate Miocene
337 climatic changes, the origins of the Drakensberg and Tropical African high mountains, *Erica's* area of

338 first establishments in Africa, are more recent, with uplift in these regions creating montane habitats
339 from the Miocene onwards (McCarthy & Rubidge, 2005).

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

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

361 Widespread species such as *E. cerinthoides* and *E. caffra*, found in the Cape and Drakensberg, and *E.*
362 *arborea*, found in Europe and Tropical Africa (Désamoré & al., 2011; Gizaw & al., 2013), are
363 exceptional in *Erica*. Almost all extant species are restricted to just one of the areas as defined here
364 (including species such as *E. silvatica* and *E. benguelensis* that are widespread across disjunct areas
365 within Tropical Africa), and species radiations leading to most of the present day diversity of *Erica*
366 were within single areas (Pirie & al., 2016). This suggests that species distributions were restricted
367 throughout the evolution of the *Erica* African/Madagascan clade, and that the areas remained
368 isolated during this period (i.e. the last c. 15 Ma; Pirie & al., 2016). We would also argue that it lends
369 credibility to results obtained under DEC+J, in which some range shifts were treated as cladogenetic
370 dispersal events (instead of by inferring seemingly implausible widespread distributions), despite
371 arguable drawbacks in the implementation of that model (Ree & Sanmartín, 2018).

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

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

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635

636 **Figures**

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

644

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

652

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

661 **Appendices**

662 **Appendix 1: Methods: occurrence data**

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

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

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

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

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

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

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

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

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

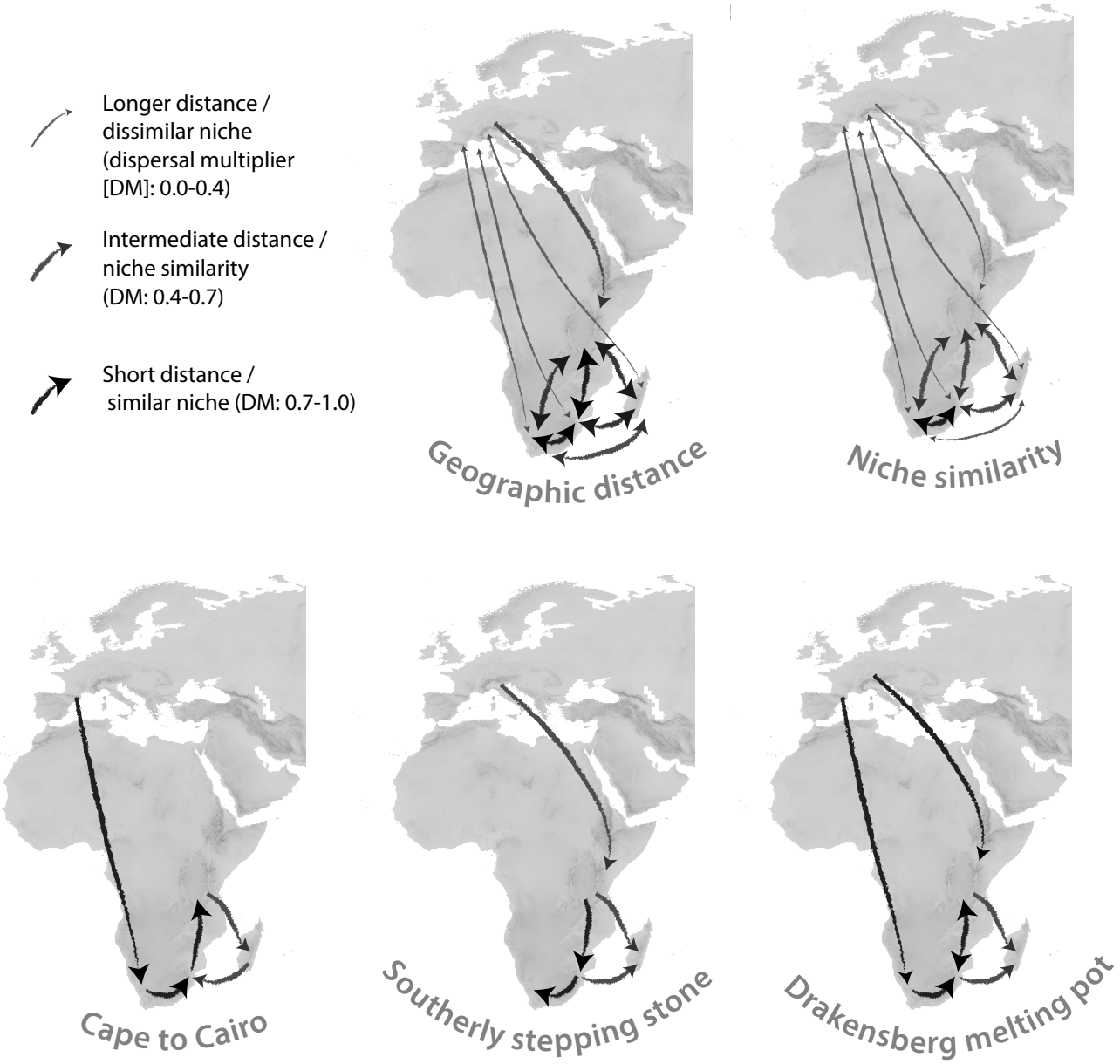
680 **Appendix 11: Results: Number of cladogenetic dispersal events (mean and standard deviation of all**
681 **observed jump 'j' dispersals) averaged from 50 biogeographical stochastic mappings under the best**
682 **inferred model using the best tree.**

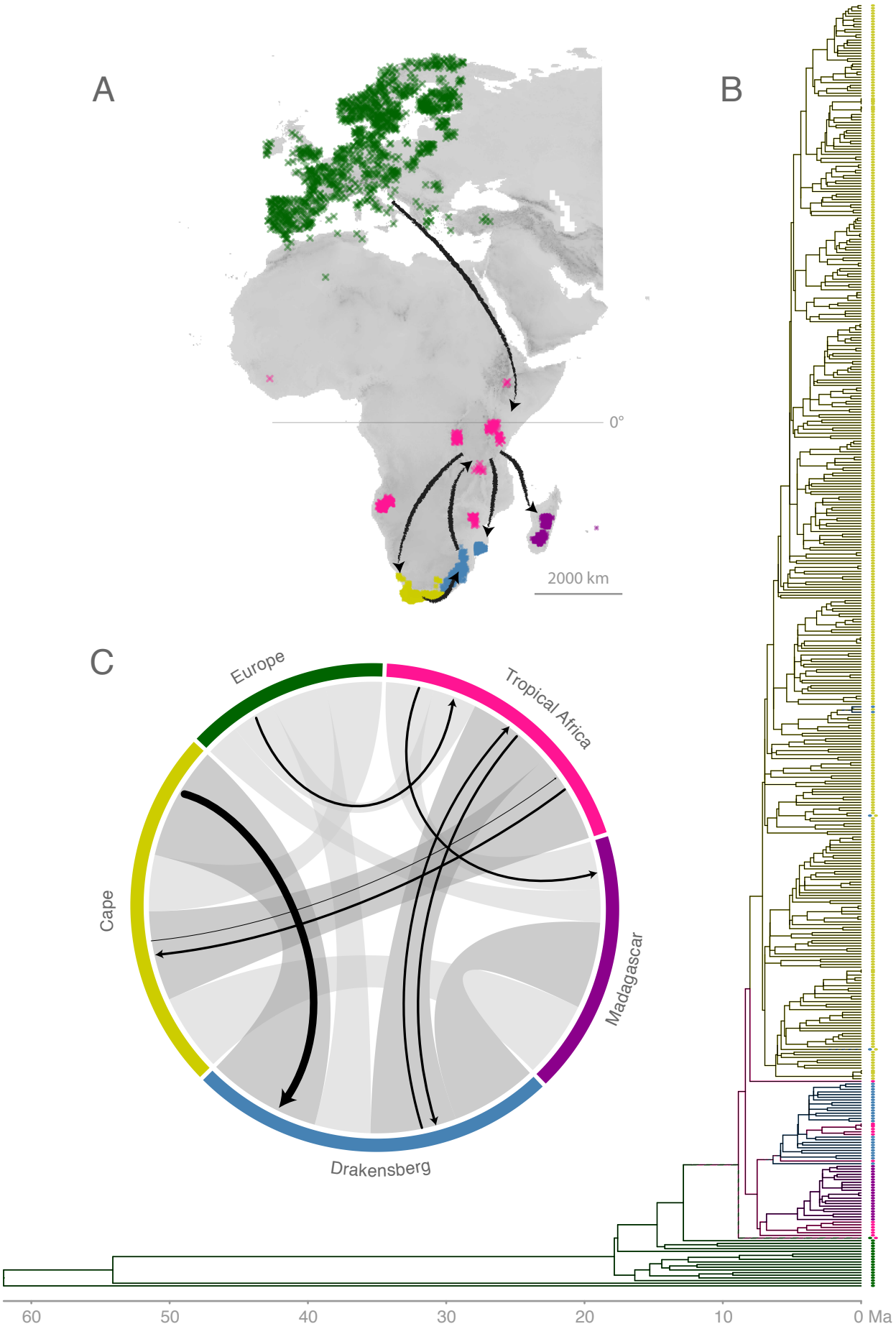
683 **Appendix 12: Results: Number of all dispersal events (mean and standard deviation of all observed**
684 **anagenetic 'a', 'd' dispersals, PLUS cladogenetic founder/jump dispersal) averaged from 50**
685 **biogeographical stochastic mappings under the best inferred model using the best tree.**

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

691 **Madagascar (M); light blue for Drakensberg (D); red for Cape (C); and further colours for**

692 **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