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; and 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 radiations.

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 distribution pattern of the more than 800 *Erica* species across Europe and Africa provides an opportunity to disentangle the effects 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.

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" (Sanmartín et al., 2010; Pokorny et al., 2015), or the "African arid corridor" hypothesis (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 alpine-like 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). The interplay between geographic distance and ecological suitability may be a decisive factor in the biogeographic history of plants (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).

In this paper, we ask whether and to what extent geographic proximity or climatic niche similarity constrained the colonisation of the Afrotemperate by *Erica*. Until recent work (Pirie, Oliver & Bellstedt, 2011; Pirie et al., 2016), too little was known of the phylogenetic relationships of the 97%

97 of *Erica* species outside Europe to be able to address such questions. Specifically, we test six
98 biogeographic models, as illustrated in Fig. 1: Three that test the influence of geographic distance,
99 climatic niche similarity, and the combination of both; and three differing stepping stone models that
100 each imply geographical distance effects promoting dispersal predominantly between adjacent
101 areas: northerly "Cape to Cairo", "Southerly stepping stone" and a model that invokes elements of
102 both, the "Drakenberg melting pot" hypothesis.

103

104 **Materials and Methods**

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

122 *Defining the pure-distance and the niche-based models:* Five biogeographic areas of the *Erica*
123 distribution were defined following Pirie & al. (2016): Europe (including northern Africa); Tropical
124 Africa (TA); Madagascar; Drakensberg; Cape. We obtained occurrence data for *Erica* species from our
125 own collections, and from PRECIS (http://newposa.sanbi.org/) and GBIF (https://www.gbif.org/)
126 databases. We curated the species occurrence data by removing obviously erroneous locality data,
127 duplicated records, and records with imprecise occurrence data (coordinates with ≤ 3 decimal places,
128 many of which represented centroids of quarter degree squares which were originally represented in
129 PRECIS), but did not further consider the source of or information on the precision of the
130 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'). To do so, we assigned the species to one of the five biogeographic areas. We assessed the area ranges around the occurrences of all species in a biogeographic area using an arbitrarily set buffer of c. 1° lat/lon in radius and 50 m elevation around the individual 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 and ecological conditions of the species' distribution in a respective biogeographic area. Solely these area ranges, which include up to several thousands of spatial points, were used in the subsequent analyses to calculate geographical and ecological distances.

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 buffered 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).

Finally, to consider both geographical and environmental distances in a joint model, we used two rate multiplier matrices, representing both climatic niche and physical distance (converted into probabilities; see above), as input.

165 *Biogeographic model testing and ancestral area reconstruction:* We used BioGeoBEARS (Matzke,
166 2013) for parametric model testing, whilst aware of the debate surrounding these models and their
167 comparison (Ree & Sanmartín, 2018; see Results and Discussion). The above defined biogeographic
168 models (Fig 1) were parameterized using different dispersal rate multipliers (see below and Appendix
169 3) and compared to null models that do not incorporate any constraints. As input data we used the
170 rate-smoothed ML phylogeny reduced to one tip per sampled species (Pirie & al., 2016; the "best
171 tree"), a file delimiting the distributional range of species, and a file indicating connectivity/distance
172 between the different areas of the *Erica* distribution (varying for the different biogeographic models;
173 Fig. 1, Appendix 3). Model fit of the different nested and non-nested models was tested using the
174 Akaike Information Criterion (AIC) and the delta AIC (Burnham & Anderson, 2002). For model testing
175 we additionally used nine trees from the RAxML bootstrap analyses of Pirie & al. (2016) of the same
176 dataset (rate-smoothed using the ape package in R; Paradis & al., 2004). These trees were selected to
177 represent the possible resolutions of phylogenetic uncertainty between the geographically restricted
178 major clades (Appendix 4), but were otherwise chosen randomly with respect to topologies and
179 branch lengths. All hypotheses were implemented with combinations of DEC, Bayarea-like or DIVA-
180 like models, with or without allowing long distance dispersal (the "+J" model of Matzke, 2014). We
181 focus on DEC and DEC+J models because these generally fit the data better than Bayarea-like or
182 DIVA-like models.

183 Prior to comparing the different biogeographic hypotheses, we tested whether an unconstrained
184 model fitted the data better than a) restricting the maximum number of areas at nodes to two;
185 and/or b) implementing an adjacent area matrix (Appendix 3; Results). The Southerly stepping stone,
186 Cape to Cairo, and Drakensberg melting pot hypotheses were then run under a range of different
187 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
188 nine bootstrap trees with dispersal multipliers of 0.01, 0.1, 0.25 and 0.5) to test whether these
189 arbitrary values influenced the results. For niche- and distance-based biogeographic models
190 Schoener's *D* values and geographic distances scaled to probabilities (see above) were used directly
191 as dispersal multipliers (Appendix 3). We also assessed the impact on model fit (given the best fitting
192 model) of a number of different values for the parameter "w", which is an exponent for the dispersal
193 multipliers (which otherwise was fixed to "1"; Appendix 3); and coding of *E. arborea* as European
194 (following Mugrabi de Kuppler et al., 2015), rather than as widespread between Europe and Tropical
195 Africa. Further details and example files for the BioGeoBEARS analyses are presented in Appendix 3.

196 *Estimating dispersal rates*: For the best models under both DEC+J and DEC, given the best tree, we
197 estimated the number and type of biogeographic events across the clade using Biogeographical
198 Stochastic Modelling (BSM) as implemented in BioGeoBEARS (Matzke, 2014). BSM simulates histories
199 of the times and locations of dispersal events. Frequencies were estimated by taking the mean and

200 standard deviation of event counts from 50 BSMs. We also compared the results to that of simple
201 parsimony optimisation using Mesquite v3.31 (Maddison & Maddison, 2006), under the assumption
202 that LDD events are simply rare (Pirie et al., 2012). We incorporated phylogenetic uncertainty by
203 summarising the results over the complete sample of 252 RAxML bootstrap trees adapted from Pirie
204 & al. (2016), and coding *E. arborea* either as widespread between Europe and Tropical Africa or
205 European (Appendix 5).

206

207
208 **Results**

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

220 *Biogeographic model testing:* DEC/DEC+J models generally fit the data better than Bayarea-like or
221 DIVA-like models. DEC+J models generally fit the data better than equivalent DEC ones (Appendix 8).
222 Under DEC+J, models including an adjacent area matrix fitted the data better than those without
223 constraint to dispersal. We additionally fixed the maximum number of ancestral areas to two,
224 increasing the speed of the analyses without negatively impacting model fit. Under DEC, models with
225 maximum areas at nodes restricted to two fitted the data better than those without constraint to
226 ancestral ranges. Under both DEC+J and DEC, geographic distance fitted the data better when
227 translated into dispersal rate multipliers (0-1) than when scaled linearly or exponentially (Appendix
228 8); we therefore focus on models using the probabilities, referring to them simply as "geographical
229 distance". The DEC +J results in general do not show the flaws as reported by Ree and SanMartin
230 (2018). For example, the values for range expansion (parameter d) were similar and low (0.0030 and
231 0.0027 respectively; Appendix 9). Under DEC+J, cladogenetic dispersal (parameter j) was 0.0024, i.e.
232 lower than d and much lower than the maximum permitted value (3).

233 Under DEC+J given the best tree, the Drakensberg melting pot, geographic distance, and southerly
234 stepping stone models revealed the lowest AIC and highest log-likelihood scores; under DEC the
235 Drakensberg melting pot model alone scored best, but with higher AIC (141 compared to 131 given
236 DEC+J; Appendix 8). Adopting DEC+J as the better fitting model, we assessed the results given
237 phylogenetic uncertainty represented by selected bootstrap trees. The combined niche-geographic
238 distance hypothesis was often among the best fitting models (deltaAIC <2 given eight of nine trees),
239 scoring better than pure distance (deltaAIC <2 for five trees), or niche similarity (deltaAIC <2 for four
240 trees) alone. The Cape to Cairo model generally fitted better than most other biogeographic
241 scenarios (deltaAIC <2 for eight of nine trees, compared to Drakensberg melting pot (deltaAIC <2 for
242 two of nine trees) and southerly stepping stone (not amongst the best fitting models); Table 1;
243 Appendix 8).

244 *Ancestral area reconstruction*: Under DEC+J, irrespective of best fitting model or phylogenetic
245 uncertainty, we infer a colonisation path of *Erica* from Europe to the Cape via an initial migration to
246 Tropical Africa. When *E. arborea* is treated as widespread between Europe and Tropical Africa, the
247 common ancestor of the African/Madagascan clade is inferred to have been similarly widespread.
248 When *E. arborea* is treated as ancestrally European, dispersal from Europe to Tropical Africa is
249 inferred without a transitional widespread distribution. Under DEC, the colonisation path to the Cape
250 is also via an initial migration to Tropical Africa, then a widespread distribution between Tropical
251 Africa and the Cape, followed by an extinction in Tropical Africa. Whether *E. arborea* is treated as
252 widespread between Europe and Tropical Africa or not, the common ancestor of the
253 African/Madagascan clade is inferred to have been similarly widespread between Europe and
254 tropical Africa. Ancestral area reconstructions given the best tree under the best fitting models
255 (DEC+J and DEC) are presented in Appendix 13. Overall, ancestral areas inferred under parsimony
256 were consistent with those inferred under parametric models (more so with those under DEC+J,
257 given that widespread distributions are not incorporated into standard character optimisation), with
258 the numbers and directions of shifts unaffected by phylogenetic uncertainty.

259 The vast majority of biogeographic events inferred using BSM under both DEC+J and DEC were
260 within-area speciation (97.15 % and 96.26% respectively; Appendix 9). Under DEC+J, few range
261 expansion events were inferred between Europe and Tropical Africa and between Tropical Africa and
262 the Drakensberg region, with most between Cape and the Drakensberg regions (Appendix 10).
263 Dispersal rates between area ranges inferred under BSM are summarised in Fig. 2C. A single founder
264 event (parameter j) was inferred from Tropical Africa to the Cape region, with fewer events between
265 the Drakensberg and Tropical Africa and between Tropical Africa and Madagascar. Overall, most
266 founder events took place from Tropical Africa (Appendix 11). In addition to the most commonly
267 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 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 "Drakensberg melting-pot" mostly fit the data better than "Southerly stepping stone", 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 climatic niche, were consistently prominent in our results. Of the distance models, the combination of geographical distance and niche similarity fit the data well, and given the phylogenetic uncertainty, often better than either of these factors individually or the stepping stone models. Of the nine range expansion events that we inferred (DEC+J, best tree, best model), seven respectively were between adjacent areas or between areas with similar niches (where "similar" is arbitrarily defined as a pairwise Schoener's $D > 0.5$; Fig. 2). Overall, this represents striking evidence for geographical and ecological distance constraining past and present distributions of *Erica* species, similar to that inferred for other Mediterranean climate plant groups (Skeels & Cardillo, 2017). Irrespective of model fit, the sequence of dispersal events that we inferred from ancestral area reconstructions, based on both the set of best fitting parametric models and a parsimonious interpretation of the infrequent dispersal events (Fig. 2), does resemble a "Drakensberg melting-pot" scenario. The Drakensberg acted as a sink for dispersals from the adjacent Cape and Tropical African regions, but not as a stepping stone (or indeed a "springboard"; Galley & al., 2007).

302 Cape lineages found in the Drakensberg have not dispersed to Tropical Africa, and neither have
303 Tropical Africa lineages found in the Drakensberg dispersed further to the Cape. This is unexpected,
304 not only because of the low distances and high niche similarities involved, but also because of the
305 equivalent events inferred in other similarly distributed plant groups (Galley et al., 2007). Striking in a
306 different way are three unique events: the single dispersals from Europe to Tropical Africa, out of
307 Tropical Africa to the Cape, and out of Tropical Africa to Madagascar, which were each over much
308 longer distances. The dispersals to Tropical Africa and to Madagascar both involved large shifts in
309 niche (Schoener's D of 0.298 and 0.274 respectively); that to the Cape, borderline so (Schoener's D of
310 0.560; Fig. 2). Notably, the dispersals to tropical Africa and to the Cape coincided with clear increases
311 in diversification rate (Pirie et al., 2016).

312 Potential explanations for these apparent exceptions to the general importance of distance and
313 climatic niche might be found in the context of the changing climates and geology of the African
314 continent during the timeframe of the *Erica* radiation. The summer-arid climate of the present day
315 Cape has been linked to the establishment of the cold Benguela current off the south-west African
316 coast in the mid Miocene 14-10 Ma (Marlow et al., 2000; Zachos et al., 2001). Evidence from pollen
317 deposited in nearby marine sediments shows an accumulation of typical Cape lineages since roughly
318 the same time, including Ericaceae (Dupont et al., 2011), supported by further evidence from recent
319 dated phylogenies both for the ages of clades in the Cape (e.g. Verboom & al., 2009; Hoffmann & al.,
320 2015) and the origins of fire adapted lineages (Bytebier et al., 2011). The gradual change from a more
321 tropical to a mesic flora and initiation of a regular fire regime in south-western Africa might be
322 ecological changes important for the establishment of *Erica* in the Cape. Whilst the mountains of the
323 Western Cape, home to much of the *Erica*-dominated fynbos vegetation, long predate Miocene
324 climatic changes, the origins of the Drakensberg and Tropical African high mountains, *Erica's* area of
325 first establishments in Africa, are more recent, with uplift in these regions creating montane habitats
326 from the Miocene onwards (McCarthy & Rubidge, 2005).

327 Thus, shifting climates and mountain building created an archipelago of temperate islands across
328 sub-Saharan Africa that were available for colonisation by plants able to tolerate the novel
329 conditions. These included *Erica* species, which had begun to diversify c. 30 Ma in the Northern
330 Hemisphere (Pirie et al., 2016), and which as a clade are characterised by drought resistant leaves
331 (Van Wilgen, Higgins & Bellstedt, 1990) as well as adaptations to post-fire regeneration (Ojeda,
332 1998). However, our analyses of the climatic niches of *Erica* species in their different biomes suggests
333 that despite these pre-existing drought and fire adaptations, colonisation of new areas by *Erica*
334 involved further adaptation to rather different climatic conditions, as inferred for tropical alpine
335 *Hypericum* in South America (Nürk, Michling & Linder, 2018) and hypothesised for tropical high
336 alpine plants in general (Gehrke, 2018). In this context, biome shifts and increased diversification

rates may be linked: the open field presented by these newly formed, isolated, temperate habitats may have facilitated both the chance establishment of suboptimally adapted plants and their subsequent *in situ* shift into new adaptive zones, promoting accelerated diversification.

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

Widespread species such as *E. cerinthoides* and *E. caffra*, found in the Cape and Drakensberg, and *E. arborea*, found in Europe and Tropical Africa (Désamoré & al., 2011; Gizaw & al., 2013), are exceptional in *Erica*. Almost all extant species are restricted to just one of the areas as defined here (including species such as *E. silvatica* and *E. benguelensis* that are widespread across disjunct areas within Tropical Africa), and species radiations leading to most of the present day diversity of *Erica* were within single areas (Pirie & al., 2016). This suggests that species distributions were restricted throughout the evolution of the *Erica* African/Madagascan clade, and that the areas remained isolated during this period (i.e. the last c. 15 Ma; Pirie & al., 2016). We would also argue that it lends credibility to results obtained under DEC+J, in which some range shifts were treated as cladogenetic dispersal events (instead of by inferring seemingly implausible widespread distributions), despite 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 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 niche 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 with large shifts in 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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609

610 **Figures**

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

618

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

626

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

Appendices

Appendix 1: Methods: occurrence data

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

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

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

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

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

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

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

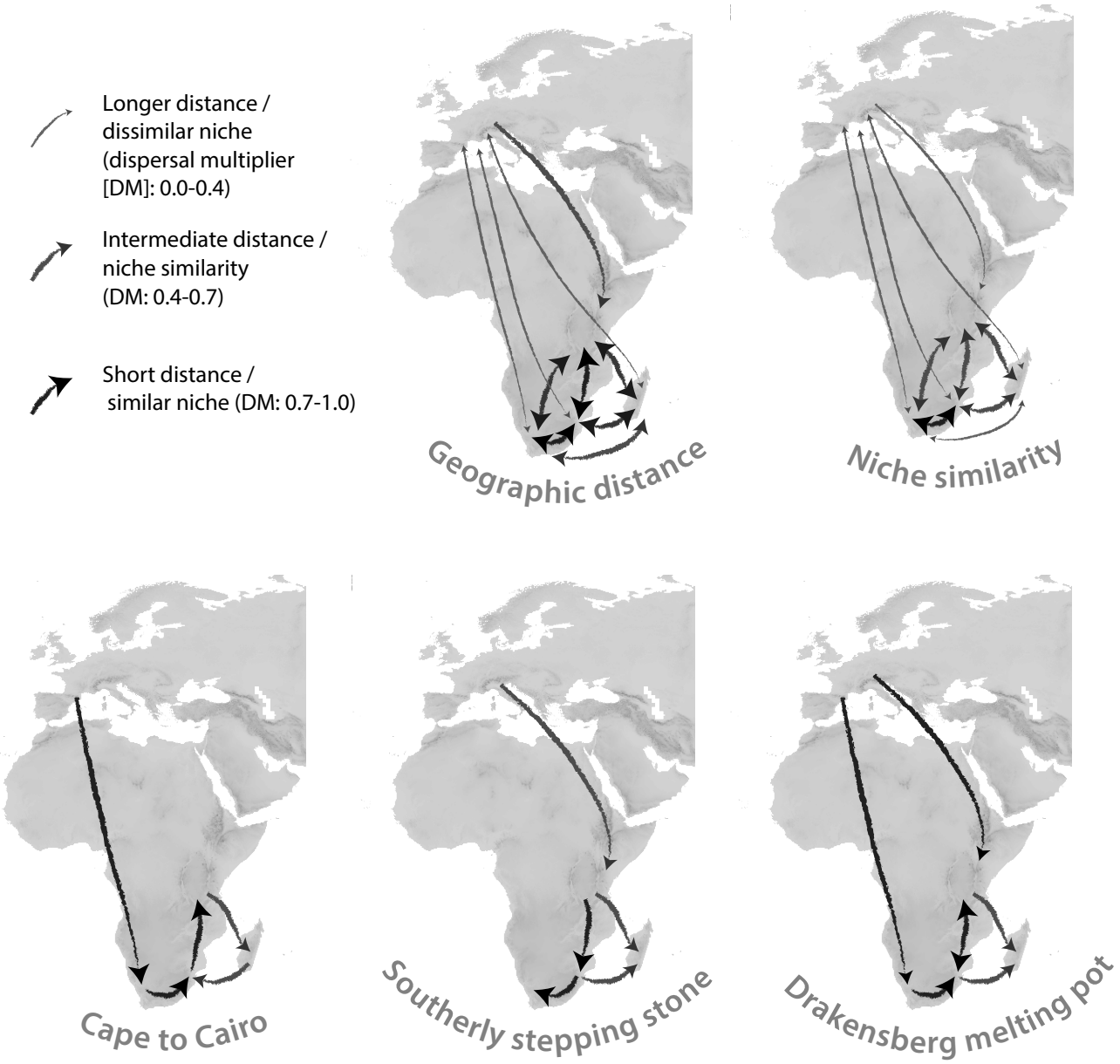
Appendix 9: Results: Summary of event counts from 50 BSMs under the best inferred model using the best tree

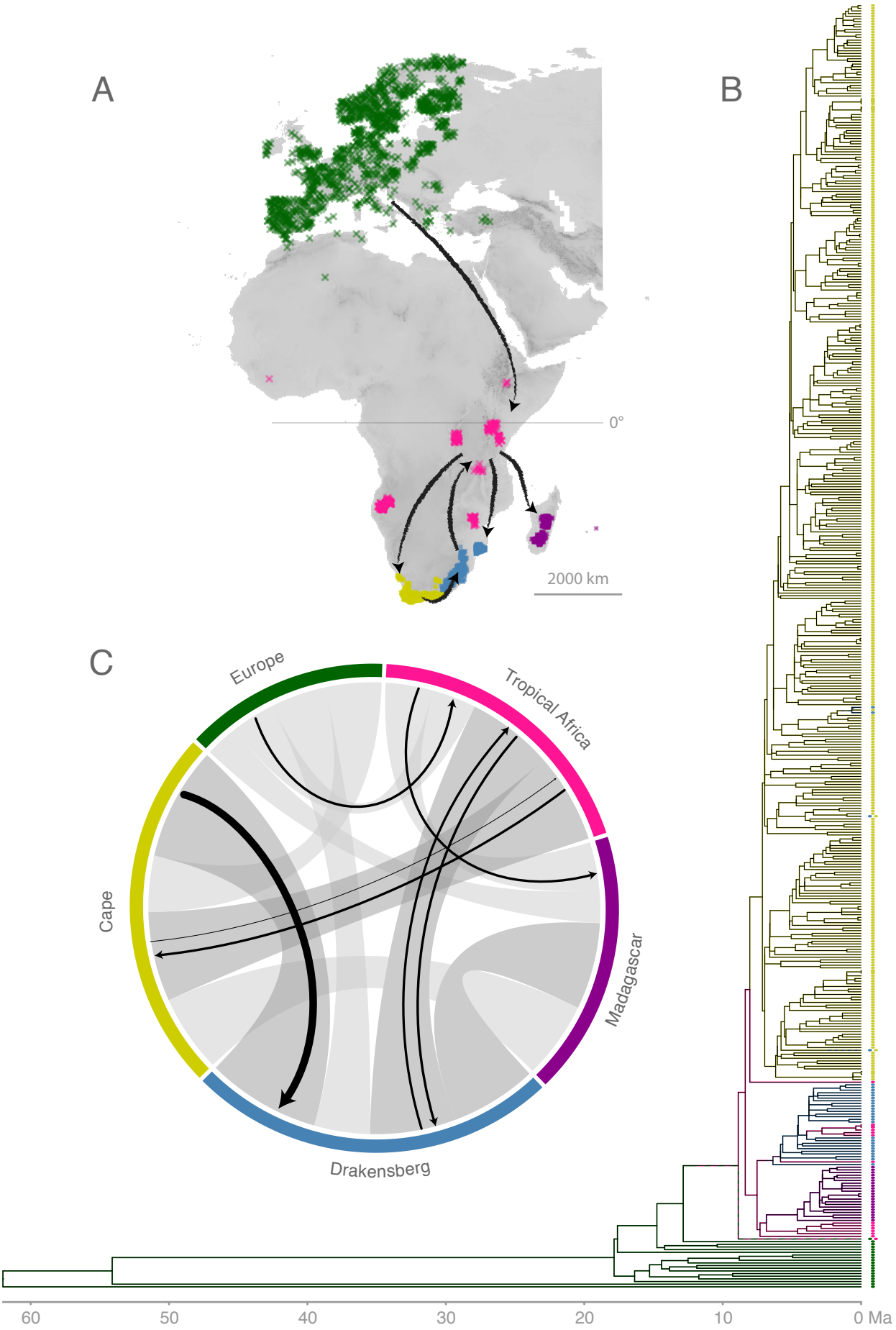
Appendix 10: Results: Range-expansion dispersal (all observed "d" dispersals). Mean and SD presented from 50 BSMs under the best inferred model using the best tree

Appendix 11: Results: Cladogenetic dispersal (mean of all observed jump 'j' dispersals) from 50 BSMs under the best inferred model using the best tree

Appendix 12: Results: ALL dispersal (mean of all observed anagenetic 'a', 'd' dispersals, PLUS cladogenetic founder/jump dispersal) from 50 BSMs under the best inferred model using the best tree

Appendix 13: Ancestral area reconstructions given the best tree under the best fitting models given A: DEC+J; B: DEC


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 I Areas (spatial sample defining area ranges, Fig. S1.1)
B I Stochastic map & ancstates: DCE+J (M0), single stochastic character mapping, n=1, global optim, 2 areas max. d=0.0028; e=0; j=0.0017; LnL=−62.51
C I Climate similarity between areas (ecospat, hypervolume corrected pairwise climate similarity [Schoener's D {median axes 1+2} ≥ 0.5: grey40%, D < 0.5: grey20%], Table S7) & **Dispersal rates** between areas (biogeobears, Table S12), proportional.