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/or 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 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 (TA); 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 hence 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 TA. They are also separated by considerable geographic distances, isolated by expanses of inhospitable habitats and/or ocean.

Similar distribution patterns across Europe and Africa are observed in different plant groups, and biogeographic scenarios have been proposed to explain these similarities, particularly in the context of changing geological and climatic conditions of the Miocene to present day. Plants adapted to different habitats respond differently to changing environmental conditions (Mairal, Sanmartín & Pellissier, 2017; Chala et al., 2017). Accordingly, some scenarios emphasise vicariance processes whilst other invoke concerted patterns of LDD. Examples of the former are the "Rand Flora" (Sanmartín et al., 2010; Pokorny et al., 2015), or the "African arid corridor" (Verdcourt, 1969; White, 1983), which might apply to arid adapted plant groups for which past distributions have been more contiguous (Bellstedt et al., 2012). The latter might instead apply to plants adapted to habitats that remained largely isolated over time, such as the more mesic temperate or alpine-like habitats of the "sky islands" of East Africa (Gehrke & Linder, 2009; Gizaw et al., 2013, 2016).

One such 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*: southerly stepping stone dispersal. Both scenarios imply that dispersal between adjacent areas/over shorter distances is more frequent. This may be true, and distance alone could conceivably be more important than directionality (Linder et al., 2013). However, the probabilities of LDDs are hard to model (Higgins & Richardson, 1999; Nathan, 2006). LDD events also involve successful establishment in more or less distinct environments. This may be a decisive factor in the biogeographic history of plants (Donoghue, 2008; Carvajal-Endara et al., 2017), so much so that clades of different ages (Pokorny et al., 2015) and/or origins, but with similar ecological tolerances, might show convergence to similar distribution patterns (Gizaw et al., 2016).

Until our recent work (Pirie, Oliver & Bellstedt, 2011; Pirie et al., 2016), too little was known of the phylogenetic relationships of the 97% of *Erica* species outside Europe to be able to test such hypotheses. In this paper, we ask whether geographic proximity or niche similarity constrained the colonisation of the Afrotemperate by *Erica*. Specifically, we test five biogeographic hypotheses, as illustrated in Fig. 1: A pure geographic distance model; a niche similarity model, implying colonisation of areas with the most similar climatic niche; and three differing stepping stone models that each imply geographical distance effects promoting dispersal predominantly between adjacent areas.

Materials and Methods

Phylogenetic hypothesis: Analyses were based on phylogenetic trees presented in Pirie & al. (2016), which represent c. 60% of the c. 800 species of *Erica* from across their geographic range and DNA sequences from multiple plastid markers and nuclear ribosomal (nrDNA) internal transcribed spacer (ITS). Pirie & al. (2016) identified a "Cape clade" that included all but one of the sampled species of *Erica* found in the CFR. The single exception was *E. pauciovulata*, which was placed within a polytomy including the Cape clade and other Afrotemperate lineages. Preliminary results based on additional sampling including nrDNA ETS (Pirie et al. in prep.) confirm the monophyly of Cape clade including *E. pauciovulata*, and we therefore exclude this taxon from biogeographic analyses to avoid inferring an independent colonisation of the CFR as a result of its uncertain position.

Defining the pure-distance and the niche-based models: Five biogeographic areas of the *Erica* distribution were defined following Pirie & al. (2016): Europe (including northern Africa); Tropical Africa (TA); Madagascar; Drakensberg; Cape. We obtained occurrence data for *Erica* species from our own collections, and from PRECIS (http://newposa.sanbi.org/) and GBIF (https://www.gbif.org/) databases. Species occurrence data was curated by removing obvious erroneous locality data, duplicated records, and records with imprecise occurrence data (coordinates with ≤ 3 decimal places), which resulted in 6818 individual occurrences representing the species in the phylogenetic trees (Appendix 1). Due to the high number of narrow endemic species in Afrotemperate *Erica* around 30% of species were represented by single records, which is not sufficient to approximate a species niche (van Proosdij et al., 2016). However, since we aimed at defining the climate conditions in and the geographic proximity between the five biogeographic areas we assigned the species occurrences to these areas, which hence were represented by multiple occurrences: Europe 4667, TA 42, Madagascar 70, Drakensberg 58, and Cape 1981 occurrences.

To incorporate in a solely distance-based biogeographic model a measure of geographic proximity of these areas we sampled all spatial points per biogeographic area that fall within a buffer of c. 1° lat/lon and 50 m elevation around the species occurrences (defining 'area ranges'; Appendix 2). The pairwise overall minimum geographic distances between the area ranges were converted into probabilities (i.e. defining the dispersal rate multipliers used in the biogeographic modelling) as a linear function of the distance between areas so that the largest distance has the smallest dispersal probability (with model intercept of 1 and a slope of -1.52^{-07}; Appendix 3).

To incorporate in a niche-based biogeographic model a measure of climatic similarity between the biogeographic areas we built a multidimensional environmental model representing the full space of climates in the global study area (Europe and Africa) using principal component analysis (PCA). We then calculated the pairwise climate similarity between the biogeographic areas as Schoener's *D*

(Schoener, 1968; ranging from 0 = no similarity to 1 = identical) while correcting for regional differences in the available climates between the areas by kernel density smoothers in the environmental space (Broennimann et al., 2012) using the protocol detailed in Appendix 2.

Ancestral area reconstruction and biogeographic model testing: Whilst aware of the debate surrounding these models and their comparison (Ree & Sanmartín, 2018), we used BioGeoBEARS (Matzke, 2013) for parametric model testing, with the above biogeographic hypotheses (models; Fig 1) defined by different dispersal rate multipliers as presented in Appendix 3 and compared to null models that do not incorporate the biogeographic hypotheses. As input data we used a dated phylogeny including one tip per sampled species (Pirie & al., 2016; the "best tree"), a file delimiting the distributional range of species, and a file indicating connectivity/distance (varying for the different biogeographic models; Fig. 1) between the different areas of the *Erica* distribution. For model testing we additionally used nine trees from the RAxML bootstrap analyses of Pirie & al. (2016) of the same dataset (rate-smoothed using the ape package in R; Paradis & al., 2004). These trees were selected to represent the possible resolutions of phylogenetic uncertainty between the geographically restricted major clades (Appendix 4).

Prior to comparing the different biogeographic hypotheses we tested whether a model without constraint to dispersal or ancestral ranges fitted the data better than setting the adjacent area matrix and maximum areas at nodes to two (as would be implied by the present day distribution of the species, which never exceed two areas). As the latter fit the data better (Results) this was implemented in subsequent models. The Southerly stepping stone, Cape to Cairo, and Drakensberg melting pot hypotheses were then run under a range of different dispersal multipliers (0.00, 0.01, 0.05, 0.075, 0.1, 0.25 and 0.5; bootstrap trees: 0.01, 0.1, 0.25 and 0.5; “+*” models [see below]: 0,01 and 0.1) to test whether these somewhat arbitrary values influenced the results. 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. All hypotheses were run with combinations of DEC, Bayarea-like or DIVA-like models with or without allowing long distance dispersal (the “+J” model of Matzke, 2014), or increasing the accuracy of the extinction rate modelling (the “+*” model of Massana & al., 2015). Model fit of the different non-nested models was tested using the Akaike Information Criterion (AIC). The parameter “w”, which is an exponent for the dispersal multipliers, was fixed to “1”. A free “w” parameter can help to remove some of the subjectivity of dispersal multipliers by optimising the matrix but there are also some issues finding the optimal maximum likelihood using a free “w” parameter (http://phylo.wikidot.com/biogeobears#toc20). Example files for the BioGeoBEARS analyses are presented in Appendix 3.

For the best model given the best tree only, we estimated the number and type of biogeographic events using Biogeographical Stochastic Modelling (BSM) as implemented in BioGeoBEARS (Matzke, 2014). BSM simulates histories of the times and locations of dispersal events. Frequencies were estimated by taking the mean and standard deviation of event counts from 50 BSMs. Those were calculated using the results of the biogeographic modelling for the best model. Mugrabi de Kuppler et al. (2015) inferred reticulation in Europe between ancestors of *E. lusitanica* and *E. arborea* on the basis of gene tree incongruence. This incongruence led Pirie & al. (2016) to exclude *E. lusitanica* from the combined analyses of plastid and nuclear DNA sequences used here, whereby the evidence that it presents for a European origin of *E. arborea* was inevitably lost from these analyses. We therefore performed a further BSM analysis coding *E. arborea* as European, rather than as widespread between Europe and TA, to test the potential impact on our results of a European ancestral area for the species.

We also compared the results to that of simple parsimony optimisation using Mesquite v3.31 (Maddison & Maddison, 2006), under the assumption that LDD events are simply rare (Pirie et al., 2012), incorporating phylogenetic uncertainty by summarising the results over the complete sample of 252 RAxML bootstrap trees adapted from Pirie & al. (2016), and coding *E. arborea* either as widespread between Europe and TA or European (Appendix 5).

Results

Climatic niche-based model: The environmental space used to approximate the climatic similarity between biogeographic areas explained > 88% of the climate variation present in the global study area on the first two PCA axes. Despite the range of differing conditions within areas, e.g. with rainfall seasonality differing according to elevation, variation between areas was considerable. The distribution and the median values for pairwise Schoener's *D* per PCA axis for the areas are presented in Appendix 6, and for the combined axes 1 and 2 in Appendix 7. According to the latter, the Cape and Drakensberg areas are climatically most similar (*D*: 0.71) and Europe and Madagascar are most different (*D*: 0.21). Most similar to the European are the Cape and Drakensberg climates (both *D*: 0.35), and the TA climate (*D*: 0.27; Fig. 2C).

Ancestral area reconstruction and biogeographic model testing: Models including an adjacent area matrix and with maximum areas at nodes restricted to two fitted the data better than those without constraint to dispersal or ancestral ranges. Of the tested dispersal models including these constraints, DEC+J generally had the lowest AIC, nevertheless with values for the jump parameter (j) consistently lower than those for the dispersal parameter (d; Appendix 8). Given the best tree, the

Drakensberg melting pot hypothesis with a dispersal multiplier of 0.25 revealed the lowest AIC and highest log-likelihood of the different biogeographic models (the AIC values for the same dispersal hypothesis with other manual dispersal multipliers are the same but have slightly lower likelihoods; Appendix 8). Given the selected bootstrap trees, generally a pure distance model showed the lowest AIC, closely followed by either a Cape to Cairo or Drakensberg melting pot model (depending on the tree; Table 1; Appendix 8).

Ancestral areas given the different phylogenetic hypotheses and best fitting models reflect a colonisation path of *Erica* from Europe to the Cape either via an initial migration to TA (in nine of ten individual reconstructions) or directly implying LDD from Europe to the Cape (Table 1). When *E. arborea* is treated as widespread between Europe and TA, the common ancestor of the African/Madagascan clade is inferred to have been similarly widespread. When *E. arborea* is treated as ancestrally European, dispersal from Europe to TA is inferred without a widespread distribution. The AIC for the latter model is lower than that given a widespread ancestral distribution of *E. aborea* (128.8 compared to 131.0; Appendix 8).

The BSM given the best tree reveals that almost all biogeographic events were within-area speciation (97%; Appendix 9). Range changes inferred under BSM are summarised in Fig. 2C. Results of the same analyses given the nine selected bootstrap trees were very similar (results not shown). Most range expansion was inferred between Cape and the Drakensberg regions, as well as between Europe and TA and between TA and the Drakensberg region (Appendix 10). A founder event (cladogenetic dispersal, represented by "+J") was inferred from TA to the Cape region, with fewer events (mean values <1) between the Drakensberg and TA and between TA and Madagascar. Overall most founder events took place from TA (Appendix 11). The only inference of vicariance was between the Drakensberg and Cape and between TA and Madagascar (whereby the latter scenario is implausible given the timeframe). The highest rates of dispersal out of a region (source area) were found for the Cape and TA, whilst the highest dispersal rate into a region (sink area) was into the Drakensberg (Appendix 12). Dispersal rates between TA and the Drakensberg were approximately symmetrical, as opposed to those between the Cape and the Drakensberg or between Europe and TA which were asymmetrical (Fig. 2; Appendix 12). Ancestral areas inferred under parsimony were consistent with those inferred under parametric models, with the numbers and directions of shifts unaffected by phylogenetic uncertainty.

Discussion

In this study, we modelled shifts between biomes and dispersals over larger distances in the radiation of *Erica*, in order to test five hypotheses for the origins of Afrotemperate plant groups (Fig. 1). Two hypotheses concerned general factors of importance in limiting plant dispersal: distance, and similarity of climatic niche. The remaining three described specific colonisation histories 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").

The "Drakensberg melting-pot" model fit the data best for the best scoring tree and one of the nine tree topologies that we used to represent uncertainty in the *Erica* phylogeny. However, the best model given the other eight trees was derived from distance alone. This latter result echoes that of Linder & al. (2013), who showed the importance of distance in modelling dispersal between continents of the Southern Hemisphere. The positions of areas relative to one another, and the similarities in their climatic niche, were also prominent in our results: of the 11 dispersal events that we inferred, 10 were between adjacent areas and nine were 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/or ecological distance constraining past and present distributions of *Erica* species, similar to that inferred for other Mediterranean climate plant groups (Skeels & Cardillo, 2017). Nevertheless, the actual dispersal scenario that we inferred from ancestral area reconstructions, based on both the best fitting parametric models and a parsimonious interpretation of the infrequent dispersal events (Fig. 2), does most closely match the "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).

The lack of dispersal out of the Drakensberg to the Cape by TA lineages and out of the Drakensberg to TA by Cape lineages is unexpected, not only because of the low distances and high niche similarities involved, but also because of the equivalent events inferred in other similarly distributed plant groups (Galley et al., 2007). Striking in a different way are three unique events: the single dispersals from Europe to TA, out of TA (or Europe) to the Cape (Table 1), and out of TA to Madagascar, which were each over much longer distances. The dispersals to TA and to the Cape both involved larger shifts in niche (Fig. 2) and, notably, coincided with increases in diversification rate (Pirie et al., 2016).

Potential explanations for these apparent exceptions to the general importance of distance and climatic niche might be found in the context of the changing climates and geology of the African

continent during the timeframe of the *Erica* radiation. The summer-arid climate of the present day Cape has been linked to the establishment of the cold Benguela current off the south-west African coast in the mid Miocene 14-10 Ma (Marlow et al., 2000; Zachos et al., 2001). Evidence from pollen deposited in nearby marine sediments shows an accumulation of typical Cape lineages since roughly the same time, including Ericaceae (Dupont et al., 2011), supported by further evidence from recent dated phylogenies both for the ages of clades in the Cape (e.g. Verboom & al., 2009; Hoffmann & al., 2015) and the origins of fire adapted lineages (Bytebier et al., 2011). The gradual change from a more tropical to a mesic flora and initiation of a regular fire regime in south-western Africa might be ecological changes important for the establishment of *Erica* in the Cape. Whilst the mountains of the Western Cape, home to much of the *Erica*-dominated fynbos vegetation, long predate Miocene climatic changes, the origins of the Drakensberg and TA high mountains are more recent, with uplift in these regions creating montane habitats from the Miocene onwards (McCarthy & Rubidge, 2005).

Thus shifting climates and mountain building created an archipelago of temperate islands across sub-Saharan Africa that were available for colonisation by plants able to tolerate the novel conditions. These included *Erica* species, which had begun to diversify c. 30 Ma in the Northern Hemisphere (Pirie et al., 2016) and which as a clade are characterised by drought resistant leaves (Van Wilgen, Higgins & Bellstedt, 1990) as well as adaptations to post-fire regeneration (Ojeda, 1998). However, our analyses of the climatic niches of *Erica* species in their different biomes suggests that despite these pre-existing drought and fire adaptations, colonisation of new areas by *Erica* involved further adaptation to rather different climatic conditions, as inferred for tropical alpine *Hypericum* in South America (Nürk, Michling & Linder, 2018) and hypothesised for tropical high alpine plants in general (Gehrke, in press). 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 TA 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 TA (Désamore & 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 TA), 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 a DEC+J model that includes jump dispersal, 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 is 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 proximity and/or niche similarity. Distance in particular is a good predictor of dispersal frequencies, and 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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Figures

Fig. 1: Biogeographic hypotheses. The pure geographic distance model; niche similarity, implying colonisation of areas with the most similar climatic niche (Donoghue 2008); 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 based on the best fitting model. **A**) Biogeographic areas illustrated on a map detailing the "area ranges" (i.e. the buffered species occurrence data) with arrows depicting the dispersal scenario. **B**) The phylogeny of *Erica* with a representation of ancestral areas derived from a single BSM analysis based on the best tree and best scenario. **C**) Climate similarity between areas given as hypervolume corrected pairwise Schoener's *D* (detailing the median of PCA axes 1 and 2; with $D \geq 0.5$ in dark grey, and $D < 0.5$ in light grey; Table S8) with superimposed black arrows illustrating dispersal rates between areas (proportional; Table S13). Ma, million years.

Tables

Table 1: Best fitting biogeographic models given the best tree and nine selected bootstrap trees. Dispersal multipliers (DM) are indicated where relevant, as are the Log likelihood (LnL) and Akaike Information Criterion (AIC) scores for models, and the colonisation pathway to the Cape that each implies (E: Europe; T: Tropical Africa; C: Cape)

Tree	Best biogeographic model	LnL	AIC	Colonisation pathway to the Cape
Best	Drakensberg melting pot (DM: 0.05)	-62.52	131	E – E+T – T - C
	Drakensberg melting pot (DM: 0.1)	-62.52	131	E – E+T – T - C
	Drakensberg melting pot (DM: 0.25)	-62,51	131	E – E+T – T - C
1_1	Pure distance	-62.49	131	E – E+T – T - C
1_2	Pure distance	-55.48	117	E – E+T – T - C
1_o	Pure distance	-55.98	118	E – E+T – T - C
2_1	Drakensberg melting pot (DM: 0.01*)	-56.47	118.9	E - C
	Drakensberg melting pot (DM: 0.10*)	-56.47	118.9	E - C
2_2	Pure distance	-65.28	136.6	E – E+T – T - C
2_o	Pure distance	-61.86	129.7	E – E+T – T - C
o_1	Pure distance	-63.34	132.7	E – E+T – T - C
o_2	Pure distance	-59.53	125.1	E – E+T – T - C
o_o	Pure distance	-60.22	126.4	E – E+T – T - C

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

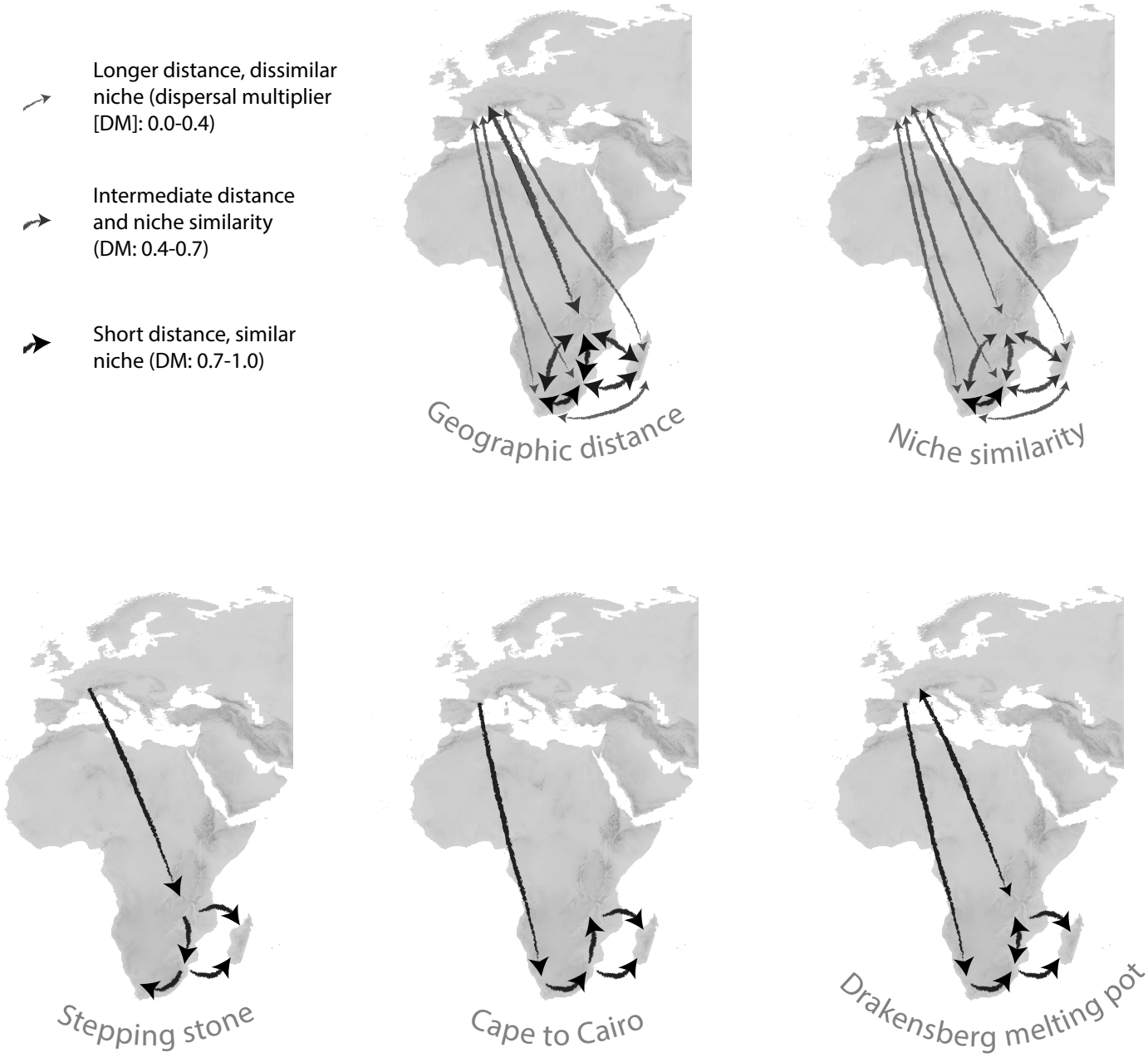
Appendix 8: Results of the different models under DEC+J (generally the better model compared to DIVA-like and BAYAREA-like-models)

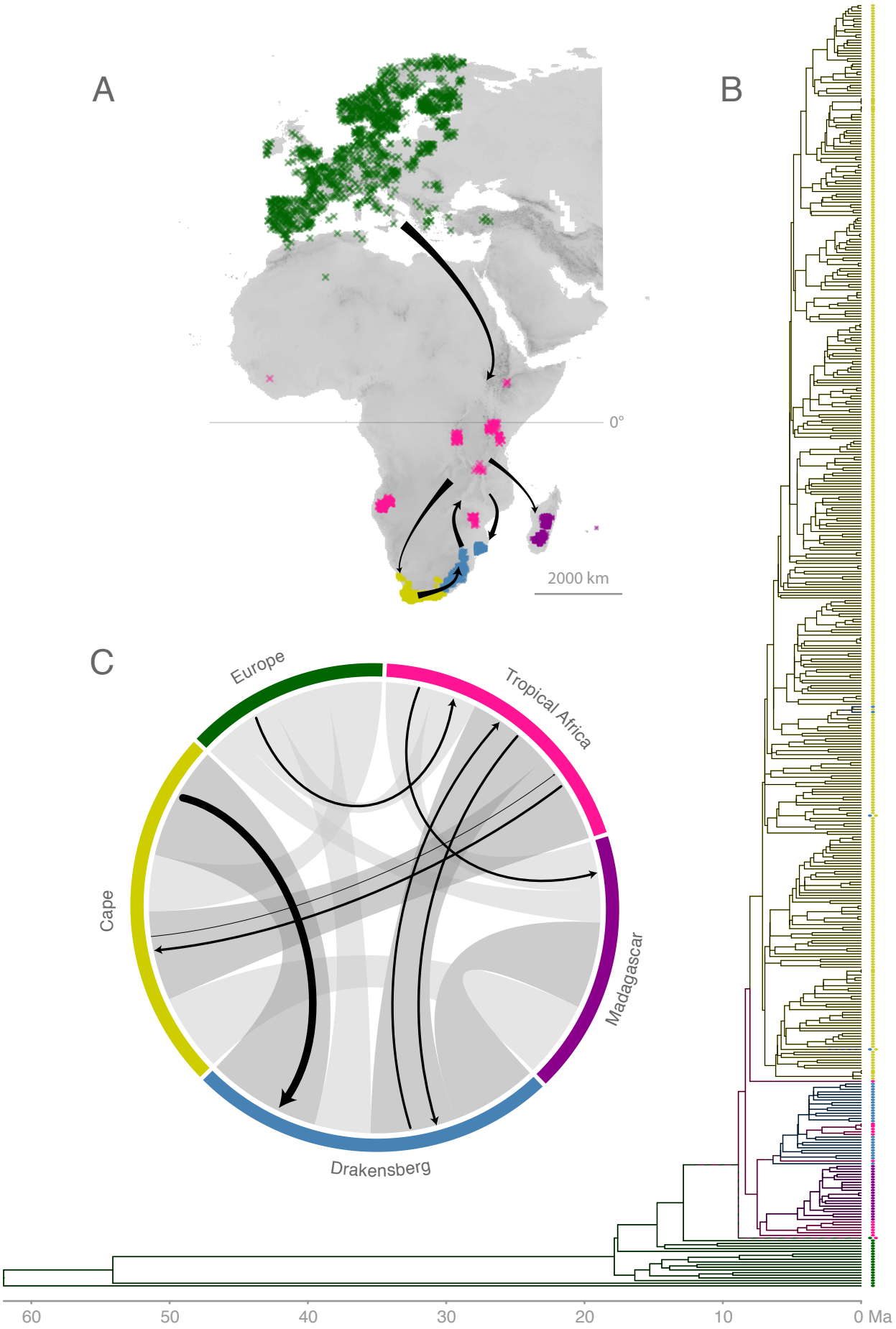
Appendix 9: Results: Summary of event counts from 50 BSMs under the best inferred model using the best tree

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


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


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