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Role of the Maloti-Drakensberg in the evolution of the southern African temperate flora: The biogeographic history of *Helichrysum* in the Great Escarpment

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ABSTRACT

We explore the role of the Maloti-Drakensberg and other major portions of the Great Escarpment in the diversification of the southern African flora using *Helichrysum* (Asteraceae, tribe Gnaphalieae), a large genus with centres of diversity in all major temperate habitats of the subregion. We use a dated Bayesian tree based on rDNA sequences from *Helichrysum* and relatives including 77% of southern African *Helichrysum* species. We infer local extinction, dispersal rates, and colonisation history of the lineage across a sample of 1000 trees under the DEC model. The *Helichrysum* clade is inferred to have arisen in the arid western regions of South Africa in the Late Oligocene, and most Succulent Karoo *Helichrysum* species are descended from the initial divergence events. There is negligible signal of later recolonisation of the arid habitat, suggesting unidirectional adaptive evolution to moister, cooler habitats. The earliest dispersal to the Maloti-Drakensberg is inferred to have occurred in the early Miocene, with the inferred route via the central summer-rainfall plateau. *Helichrysum* diversified extensively in the greater Maloti-Drakensberg region, and establishment in this area appears to underpin migrations of the lineages out of South Africa, including to the southern and northern Afrotemperate regions. Occasional dispersals to areas outside of Africa from the Maloti-Drakensberg may have seeded some of the diversifications of this clade in Madagascar, Europe, Asia, and the Americas. Our analyses recover a previously unknown role for the Central Plateau of southern Africa in cross-seeded regional radiations, possibly linked to expansion of the cold-temperate habitat during glacial maxima, although we also infer some direct migrations between the Maloti-Drakensberg and both the Succulent Karoo and Fynbos regions. A long history in the northern and eastern parts of the Great Escarpment explains the current diversity of *Helichrysum* in both the Maloti-Drakensberg region and the North-East Escarpment. While no single large radiation is recovered, there is evidence of considerable parallel *in situ* speciation in the Maloti-Drakensberg, creating an important centre of *Helichrysum* diversity and endemism. Rare recolonisation of the Fynbos Biome contributed to this important centre of *Helichrysum* diversity and endemism. The Maloti-Drakensberg has also played a key role as a recent source of floral diversity for the temperate and montane floras of southern, Central and East Africa.

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1. Introduction

The flora of southern Africa is amongst the richest of global temperate floras, estimated to include up to half the plant species richness of the African continent and more than 10% of the world's vascular plants (Germishuizen and Meyer, 2003; Linder, 2014). Estimated levels of endemism are near 70% for portions of this flora (Goldblatt, 1978; Linder, 2005), indicating a long history of *in situ* radiation. Factors thought to have facilitated the accumulation of species diversity include geographic isolation (Linder, 2003), environmental heterogeneity (Goldblatt and Manning, 2002; Verboom et al., 2015), long-term climate stability (Cowling et al., 2009; Cowling et al., 2015), and the cross-seeding of radiations within environmentally heterogeneous subregions (Linder and Verboom, 2015). Undoubtedly, the fine scale of environmental variation across the region has played a strong role, with regional habitat heterogeneity enhanced by the division of the subregion into a coastal plain, a rugged escarpment known as the 'Great Escarpment', and an elevated Central Plateau (Fig. 1). Together with gradients in temperature and precipitation, this strong regional habitat partitioning has fostered nested floristic radiations (Linder and Verboom 2015). In particular, the Escarpment margin is characterised by markedly increased precipitation and reduced temperatures relative to

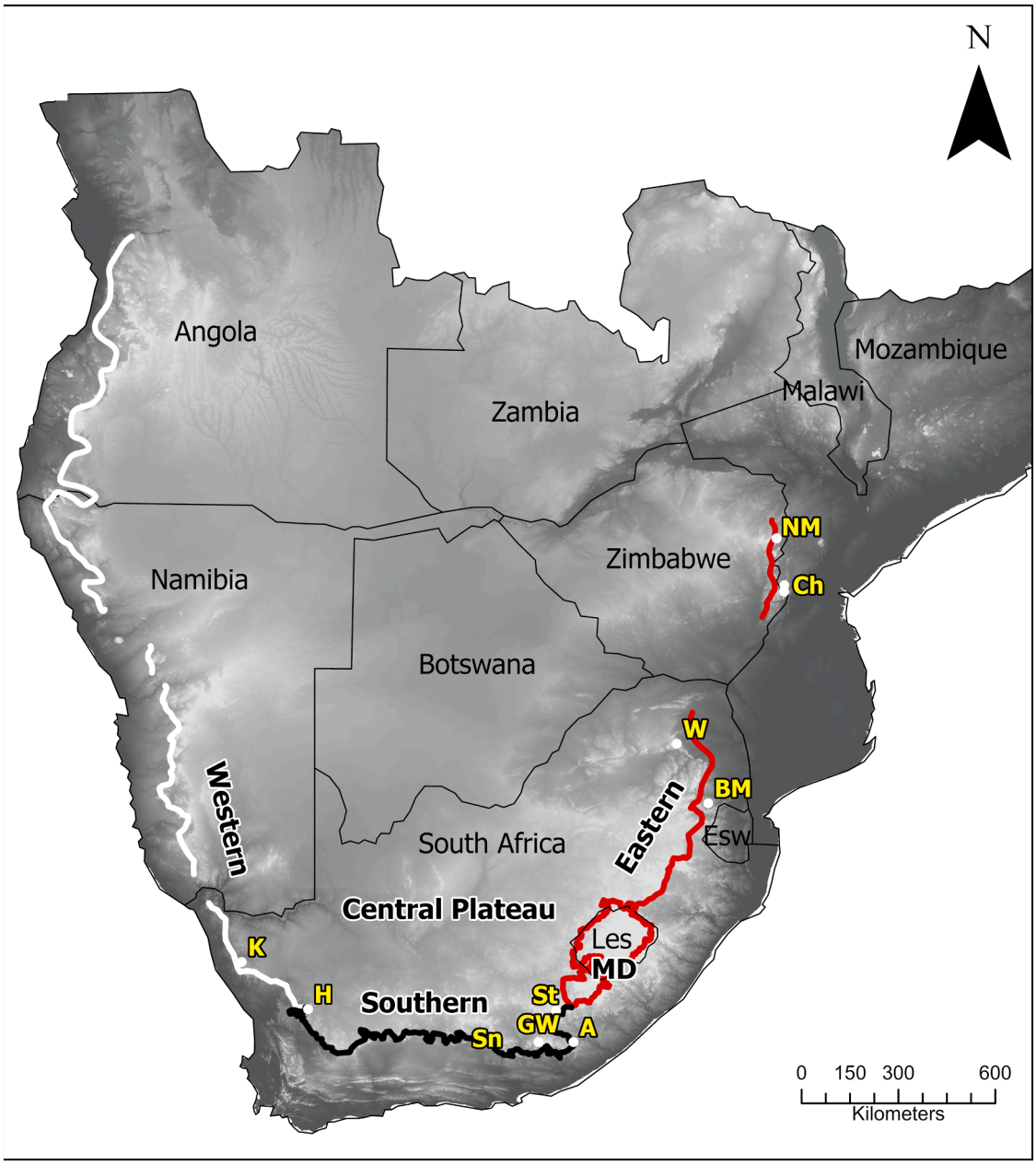

Fig. 1. Map of southern Africa showing the Central Plateau of South Africa edged by the Great Escarpment and its relationship to the Cape Fold Mountains in the south; Les = Lesotho; Esw = Eswatini. The sections of the Great Escarpment are shown: White: Western; Black: Southern; Red: Eastern, the Drakensberg range, with the highest portion being the Maloti-Drakensberg and the Manica Highlands of Zimbabwe and Mozambique. Mountains: K: Kamiesberg; H: Hantamsberg; Sn: Sneeuberg complex; St: Stormberg; GW: Great Winterberg; A: Amatholes; MD: Maloti-Drakensberg; BM: Barberton Mountainlands; W: Wolkberg; Ch: Mt Binga, highest point in Chimanimani Mts; NM: Mt. Inyangani, highest point on the Nyanga Massif.

surrounding areas, creating a swathe of cool growing-season temperate habitat along the length of southern Africa.

This 5000 km-long Great Escarpment comprises a semi-continuous mountain system along the margin of the sub-continent, formed after the break-up of Gondwana (Fig. 1; Birkenhauer, 1991; Burke and Gunnel, 2008; Moore et al., 2009). The Escarpment is deemed to have formed via passive erosion of the continental margin that, by parallel retreat, receded from the original areas of rifting (Matmon et al., 2002; Moore and Blenkinsop, 2006). Various sections of the Escarpment are recognised (Fig. 1): a western section from Angola southwards through Namibia to the Kamiesberg in the Northern Cape province of South Africa; a southern section from the Hantamsberg in the west to the Great Winterberg–Amathole mountains and Stormberg; and an eastern section including the high Drakensberg that continues northwards to the northern (previously 'Transvaal') Drakensberg Escarpment and Manica Highlands (Chimanimani and Nyanga mountains) in Zimbabwe and Mozambique (Clark et al., 2011, 2012; 2019; 2022).

The highest elevation portions of the eastern section of the Great Escarpment comprise two main centres of floristic diversity and endemism – the Maloti-Drakensberg (Carbutt, 2019) and the northern extension of the Great Escarpment, the Limpopo-Mpumalanga-Eswatini Escarpment (LMEE), which includes the Barberton Mountainlands and Wolkberg (Fig. 1), as well as some lower-lying areas (Clark et al., 2022). Both are components of the Grassland Biome of South Africa (Mucina and Rutherford, 2006). Further north, the Chimanimani-Nyanga Centre of Endemism in the Manica Highlands of Zimbabwe and Mozambique (Clark et al., 2017; Van Wyk and Smith, 2001) forms a northerly extension of the Great Escarpment (Clark et al., 2011).

The Great Escarpment reaches its highest point in north-eastern Lesotho, at 3482 m above sea level (a.s.l.; Carbutt, 2019), and the summit plateau and peaks of the Maloti-Drakensberg represent the only alpine region in southern Africa. The area above 1800 m is a long-recognised centre of floristic diversity with high endemism (Hilliard and Burtt, 1987; Van Wyk and Smith 2001; Carbutt and Edwards, 2006). Floristically, the entire Great Escarpment, but particularly the Maloti-Drakensberg region, show strong links to the hyper-diverse and highly endemic Cape Floristic Region (CFR; Hilliard and Burtt, 1987), where species richness per unit area is matched only by the richest neotropical areas (Grobler and Cowling, 2022).

The Great Escarpment also represents the southern portion of the 'afrotemperate track', a biogeographic pattern of floristic affinities across the dispersed Afromontane 'archipelago' that suggests a historical connection (Weimarck, 1941; Hedberg, 1965; Wild, 1968; Killick, 1978; White, 1978; Cowling, 1983; Linder, 1990) culminating in the CFR at the extreme southwest of the continent. An estimated 22% of plant genera from the Maloti-Drakensberg have lineages with an inferred origin in the CFR (Hilliard and Burtt, 1987). Cape elements (i.e. with strong floristic linkages to the CFR) also occur on the quartzitic outcrops of the Wolkberg Centre (Matthews et al., 1993), and on the Chimanimani Mountains and Nyanga Massif (Manica Highlands as per Clark et al., 2022). In addition, some Drakensberg elements show a disjunction between the Drakensberg and the Manica Highlands, e.g. *Craterocapsa* Hilliard & B.L.Burtt (Campanulaceae) and *Protea dracomontana* Beard (Proteaceae; Van Wyk and Smith, 2001).

The southern section of this Great Escarpment (Fig. 1), about 800 km long (Clark et al., 2011), is proposed to have acted as a corridor linking the more arid, winter-rainfall western portions with the wetter, summer-rainfall eastern parts (Weimarck, 1941; Levyns, 1952, 1964; Carbutt and Edwards, 2001; van Wyk and Smith, 2001; Clark et al. 2009; Clark et al., 2012). The southern Great Escarpment is an obvious modern geographic connection between the mountains of the CFR and the Maloti-Drakensberg, as well as between other montane or high-lying regions of southern Africa. Frequent exchanges between the hyper-diverse CFR and the Maloti-Drakensberg (e.g. Hilliard and Burtt, 1987; Galley et al., 2007) are implicated in cross-seeding regional radiations that have contributed significantly to the diversity of southern Africa (Linder and Verboom, 2015). It has been hypothesised that this escarpment region has facilitated floristic migrations, not only within South Africa but also along the 'Afromontane archipelago' (Clark et al., 2012). While the latter role has been quite extensively explored (e.g., Galley et al., 2007; Blanco-Gavaldà et al., 2023), the role of the Great Escarpment in the diversification of the flora within southern Africa has been less frequently evaluated (e.g. Clark et al., 2012).

Species-level phylogenies are an important tool for studying regional radiations and identifying cross-seeding across regions. The widespread genus *Helichrysum* Mill. (Asteraceae, tribe Gnaphalieae, subtribe Gnaphaliinae) has ~560 species distributed mainly in Africa, Madagascar, and Eurasia. However, it is not monophyletic as currently circumscribed, and includes several other nested genera, the most species-rich being the Asian and American genera *Achyrocline* Less., *Anaphalis* DC., and *Pseudognaphalium* Kirp. (Galbany-Casals et al., 2014; Nie et al., 2016; Blanco-Gavaldà et al., 2023); the entire lineage now informally called the 'HAP clade' (Smissen et al., 2011).

The HAP clade originated in the arid south-west of southern Africa (Bergh and Linder, 2009; Galbany-Casals et al., 2014; Nie et al., 2016; Andrés-Sánchez et al., 2019; Blanco-Gavaldà et al., 2023; Blanco-Gavaldà et al., 2025a, 2025b), and nearly half of all *Helichrysum* species (~245 spp.) occur in southern Africa, across a range of habitats and biomes (Hilliard, 1983; Germishuizen and Meyer, 2003) with two centres of diversity: the Greater CFR (GCFR) with ca. 89 species (Manning and Goldblatt, 2012; Snijman, 2013), and the Maloti-Drakensberg with ca. 102 spp. Within the Maloti-Drakensberg centre, *Helichrysum* also contributes the highest number of endemic species (24) of any genus (Carbutt, 2019).

Here we generate a dated phylogeny of *Helichrysum*, with sampling focussed on the southern African taxa, to explore the role of the Great Escarpment, and specifically the Maloti-Drakensberg portion, in diversification of the southern Africa temperate flora. We investigate the most likely route and mode of migration of *Helichrysum* north-eastwards within southern Africa, and the history of diversification of the lineage along the Great Escarpment. While we know that the HAP lineage originated in the arid west, many details of historical biogeography within southern Africa remain unclear, including whether range expansions were facilitated by changing climate regimes, and which geographic pathways facilitated migration. We distinguish the following biogeographic scenarios for migration of *Helichrysum* from the CFR to the Maloti-Drakensberg: (i) lineages used the southern Great Escarpment as a stepping stone north-eastward to the Maloti-Drakensberg (as suggested by Clark et al., 2012); (ii) migration occurred via the high-elevation central interior plateau of South Africa; (iii) migration occurred via the Cape coastal region to the KwaZulu-Natal (KZN) Midlands, with subsequent elevational shifts leading to colonisation of the montane and alpine zones of the Maloti-Drakensberg; (iv) alternatively, none of these routes was used, and the dominant mode was long-distance dispersal, for example, directly from the Succulent Karoo Region (SKR) to the Maloti-Drakensberg. In addition, we examine the role of the Maloti-Drakensberg in subsequent diversification of the HAP lineage, both within the southern African subregion, and beyond.

Addressing these questions in *Helichrysum* increases our understanding of potential migration routes and modes of diversification for

the species- and endemic-rich temperate flora of southern Africa and further elucidates the role of the Great Escarpment and the Maloti-Drakensberg, including the small alpine region of southern Africa, in this diversification.

2. Materials and methods

2.1. Taxon sampling

New sequences generated for this study were supplemented with published sequences to include a total of 326 taxa in the full analysis (Table S1 in Supporting Information, authorities for all species' names provided therein). For calibration purposes, and to eliminate large phylogenetic gaps in outgroup relationships, we included 26 non-Gnaphalieae outgroup species from across the subfamily Asteroideae (Asteraceae), representing the other four southern-African centred tribes Senecioneae, Anthemideae, Astereae and Calenduleae (Funk et al., 2005; Watson et al., 2020), as well as the more distant Athroismeae and the Heliantheae alliance. Within tribe Gnaphalieae, a total of 30 non-HAP clade species were included, representing the subtribe Relhaniinae and other major clades within subtribe Gnaphaliinae (Smissen et al., 2020). Our analyses incorporate 270 HAP clade taxa, including species from Africa outside the southern African subregion, Madagascar, the Macaronesian and Mediterranean regions, Asia and the Americas, and representatives of the genera known to be nested within *Helichrysum* (*Achyrocline, Anaphalis, Pseudognaphalium, Galeomma* Rauschert and *Humeocline* Anderb.; Galbany-Casals et al., 2014, Nie et al., 2016). A total of 256 *Helichrysum* species was included, of which 188 are from the southern African subregion, representing 77% of the subregion's *Helichrysum* species. Since our focus is the southern African subregion, we

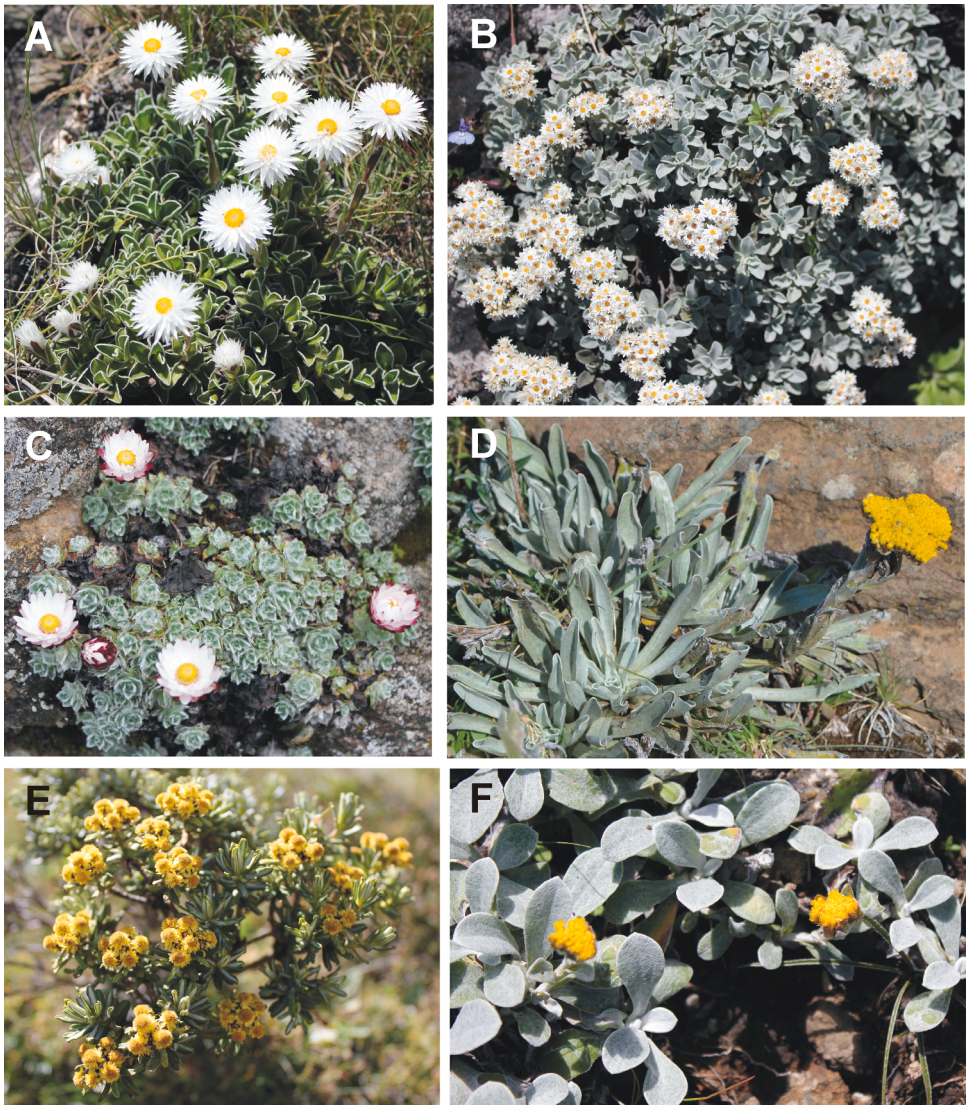

Fig. 2. *Helichrysum* species, mostly endemic and near-endemic to the Drakensberg Mountain Centre. A. *H. marginatum* (endemic mat-forming dwarf-shrub, 2440–3300 m a.s.l.), B. *H. sutherlandii* (near-endemic shrublet; 1500–3000 m a.s.l.), C. *H. milfordiae* (endemic mat- or cushion-forming subshrub, 2885–3400 m a.s.l.), D. *H. montanum* (near-endemic dwarf shrub, 1800–2500 m a.s.l.), E. *H. witbergense* (endemic perennial shrub, to ca. 3400 m a.s.l.), F. *H. evansii* (endemic mat-forming perennial, 1900–3200 m a.s.l.). Photographic credits: G.V. Cron.

used 32 placeholder species to represent groups from the Tropical East African Mountains and Madagascar, based on Galbany-Casals et al.'s (2014) phylogeny. We included 17 (71%) of the 24 endemic Maloti-Drakensberg *Helichrysum* species (Carbutt 2019), including six of the seven endemic alpine species (86%), and 32 (72%) of the near-endemic species (Carbutt and Edwards, 2006; see Fig. 2 for examples). New sequences were generated for 55 *Helichrysum* species from southern Africa.

2.2. DNA extraction, amplification, sequencing and alignment

Standard protocols for DNA extraction, amplification and sequencing were followed (see details in Appendix S1 in Supporting Information). We sequenced the nuclear ribosomal ITS and ETS regions, since plastid trees in the tribe have tended to be poorly resolved and supported (e.g., Galbany-Casals et al., 2014).

Alignment of the ITS region was straightforward, but due to missing data in some taxa the ETS region was aligned in two sections, the more variable 5' end, and the conserved 3' end (Table S2). Each section was initially aligned using the MUSCLE algorithm (Edgar, 2004) on the online EMBL-EBI Tools website (Harte et al., 2004). The resulting alignments were checked manually in BioEdit 7.0.9.0. (Hall, 1999). The software ALTER (Glez-Peña et al., 2010), accessed at http://www.sing-group.org/ALTER/, was used for conversion between nexus and fasta file formats during alignment and analysis. Due to large amounts of missing data in the selected outgroup taxa, and to alignment difficulties over large phylogenetic distances, the 5' ETS was coded as missing data for all non-HAP clade taxa.

2.3. Phylogenetic and dating analyses

Phylogenetic congruence between the ITS and ETS regions was assessed by examining separate parsimony bootstrap trees to detect ≥70 % bootstrap support for conflicting clades. Separate trees were constructed in PAUP* 4.0a (build 169; Swofford, 2003) using 1000 bootstrap replicates derived from a matrix comprising only parsimony-informative sites, with all characters equally weighted, and unordered. The separate ITS and ETS bootstrap consensus trees had very similar topologies, with no supported conflict (data not shown), so we concatenated the entire ribosomal dataset.

Absolute divergence times within the HAP clade were estimated using an uncorrelated Bayesian relaxed clock (Drummond et al., 2006) implemented in BEAST v1.8.4 (Drummond and Rambaut, 2007; Drummond et al., 2012). The molecular clock was calibrated with two fossil ages and one secondary age estimate (See Appendix S2 in Supporting Information for further details on the phylogenetic and dating analyses).

2.4. Biogeographic analysis

Nine operational biogeographic areas, mainly within southern Africa, were defined based on distribution ranges of *Helichrysum* species (Table 1; Fig. 3) as per Hilliard (1983) and updated using the Botanical Database of SANBI herbaria (BODATSA; South African National Biodiversity Institute; http://posa.sanbi.org/), Phillipson (1987), the Flora of Tropical East Africa (Beentje 2002; POWO 2023), and Flora of Zimbabwe website (https://www.zimbabweflora.co.zw), as well as specimens in the C.E. Moss Herbarium, University of the Witwatersrand, Johannesburg (J). Distribution ranges of outgroup taxa were obtained from POWO.

Our regions (Table 1, Fig. 3) are defined based on the combination of biogeographically significant areas for *Helichrysum* determined using herbarium distribution records and our taxonomic and field expertise in the group, in which both orographic and floristic concepts are used. In our final area delimitation, we adopted areas that maximise the endemism of *Helichrysum* species, although for computational reasons some areas were amalgamated, resulting in nine areas, viz., the Maloti-

Table 1
The nine operational biogeographic areas designated for reconstruction of ancestral areas (SDEC) analysis of the HAP clade in RASP (see map, Fig. 3). Number of *Helichrysum* species' occurrences in this study indicated in parentheses; * = numbers of species under-represented to accommodate analysis.

A	Maloti-Drakensberg (93)	Corresponds to the 'Drakensberg Mountain Centre' (Carbutt, 2019), areas above 1800 m in the KwaZulu-Natal and Eastern Cape Drakensberg, the Eastern Cape Witteberg, and the Maloti Mountains of Lesotho, as well as the Amathole Mts. Also included are the outlying peaks of Mounts Ngeli, Insizwa, Currie, Mahaqwa, Ntiskeni, Insizwa, Ayliff, and Zuurberg (as per the 'Eastern Mountain Region' of Phillips, 1917; Hilliard and Burtt, 1987).
B	KwaZulu-Natal (KZN) Midlands and Coastal grasslands (59)	Includes the grasslands of the KwaZulu-Natal Midlands and coastal areas, including the Transkei coastal region and Pondoland. The very few *Helichrysum* species occurring in the Albany coastal area were also assigned to this area.
C	Central Plateau (35)	This broadly-defined summer-rainfall area encompasses the Highveld Bioregion which largely comprises Nama Karoo vegetation, the Kalahari, and the Northern Namibian interior. It does not include coastal Namibia, which has more winter precipitation.
D	Core Fynbos Biome region (31)	Corresponds to the region occupied by fynbos heathland, renosterveld and coastal strandveld vegetation within the Cape Floristic Region (CFR) in the Western and Eastern Cape provinces of South Africa. Floristically, it is loosely synonymous with the 'Cape Flora'.
E	Succulent Karoo Region (SKR) (19)	This area is occupied by Succulent Karoo (SK) vegetation and corresponds to the winter-rainfall desert regions of the Succulent Karoo Biome. Included are some Nama Karoo *Helichrysum* species that extend into the SK, and occasional species in the coastal Namib desert of Namibia.
F	Southern Escarpment (27)	Covers the southern section of the Great Escarpment (see Fig. 1), i.e., the Hantamsberg, Roggeveldberge and Komsberg, Nuweveldberge, Sneeuberg, Boschberg; Great Winterberg and the Stormberg (see Clark et al., 2012).
G	'North-Eastern Escarpment' & Manica Highlands (NE Escarpment) (81)	Corresponds to the northern portion of the Eastern Great Escarpment (see Fig. 1), the Limpopo-Mpumalanga-Eswatini Escarpment (LMEE) which incorporates the Northern Escarpment (as per White, 1978), the Wolkberg, the Barberton Mountains, the Soutpansberg and the northern KZN–Mpumalanga border mountains of South Africa. Also included are the Manica Highlands (the Chimanimani and Vumba Mountains and Nyanga Massif; Fig. 1).
H	Tropical East African Mountains (and Madagascar) (17*)	This broadly defined region includes East and Central African mountains forming the Northern Afromontane archipelago from the Kitulo Plateau northward to the Ethiopian Highlands. To reduce the number of areas, we also included Madagascar here. This is justified by evidence of biogeographic links between Madagascar and the East African mountains (Blanco-Gavaldà et al., 2025a).
I	Extra-African regions (17*)	Due to our main focus on biogeographic patterns within southern Africa, we amalgamated all *Helichrysum* species occurring outside of Africa and Madagascar into a single category that includes Macaronesia, the Mediterranean region, Asia, and the Americas.

Table 2
Median and 95% highest posterior density age estimates for selected nodes, from calibrated BEAST dating analysis. All ages refer to crown nodes unless otherwise indicated. (* indicates calibrated nodes).

Nodes	(Ma) Median	95% HPD interval (Ma)
Asteroideae (root)	62.97	45.3 – 87.2
Ambrosia*-type pollen stem age	**23.46**	**22.0 – 27.6**
Gnaphalieae *	**46.55**	**32.3 – 65.2**
Relhaniinae	31.34	18.0 – 46.6
SIM clade	28.50	18.3 – 41.4
Stoebe/Elytropappus*-type pollen stem age	**9.18**	**8.5 – 10.9**
FLAG Clade	14.2	7.5 – 22.0
Gnaphalium clade	15.69	9.2 – 24.0
Australasian clade	17.65	10.7 – 25.7
HAP clade:	**25.50**	**17.7 – 35.1**
H. hebelepis clade	5.83	1.9 – 11.8
GCFR clade	17.67	12.1 – 24.9
Galeomma clade	13.24	8.2 – 20.2
H. dasymallum clade	7.53	3.8 – 12.3
H. alucense clade	6.55	3.9 – 9.7
H. rudolfii clade	2.94	1.2 – 6.0
Helichrysum type clade	4.72	3.0 – 7.0

Drakensberg (Hilliard and Burtt, 1987; Carbutt, 2019); the KZN Midlands and Coastal grasslands; the SKR; Central Plateau; Southern Escarpment; the core Fynbos Biome region (within the CFR); the NE Escarpment and Manica Highlands; Tropical East African mountains (and Madagascar); and areas outside of Africa (Table 1).

We defined the Maloti-Drakensberg to comprise the Drakensberg Mountain Centre as recently delineated by Carbutt (2019), including the Drakensberg Montane and Maloti-Alpine subcentres, but also included here the montane outliers (Mounts Mahwaqa, Currie and Ngeli) originally included in the Eastern Mountain Region of Hilliard and Burtt (1987). Since all but two of the *Helichrysum* species that occur in the Amathole mountains also occur in the Maloti-Drakensberg, and since ca. 71% of the *Helichrysum* species included here occur in both the Amatholes and the Maloti-Drakensberg, including 19 near-endemic to the Maloti-Drakensberg (Phillipson, 1987; Clark et al., 2009), we incorporated the Amathole mountains (Fig. 1) within our definition of the Maloti-Drakensberg region for the purpose of assessing biogeography in *Helichrysum*.

Of the 216 HAP clade members included in our biogeographic analysis (Table S1), the majority (192, or 89%) occur in three or fewer of our defined areas. Most taxa (118, or 55%) are endemic to a single area, 42 (19%) occur in two areas, and 32 (15%) occur in three areas. Of the nine areas, the Maloti-Drakensberg had the highest number of occurrences (93), followed closely by the NE Escarpment & Manica Highlands (81 occurrences; Table 1).

The likelihood-based statistical dispersal-extinction-cladogenesis (S-DEC) model of Bayes-Lagrange (Ree et al., 2005; Ree and Smith, 2008; Beaulieu et al., 2013) implemented in RASP v.4.2 (Yu et al. 2020) was used to infer ancestral range inheritance scenarios as well as local extinction and dispersal rates on the BEAST MCC tree and on a subset of 1000 trees from the posterior sample. We used an unconstrained model in which dispersal rates were assumed to be equal among areas. Widespread ancestral ranges were constrained to combinations of no more than three areas, assuming that ancestors were not more widespread than their extant descendants (Sanmartin, 2003). To reduce the number of 'uncertain' reconstructions where many area combinations all had low probabilities, we used the cumulative probability of occupation of an area (the sum of the probabilities of an area, over all the area combinations in which that area has a probability ≥ 0.01 in the S-DEC results). Such cumulative probabilities indicate a high likelihood that the lineage occurred in a particular area (or combination of areas), even though it may also have occupied other areas.

3. Results

3.1. Molecular phylogeny

The final alignment (TreeBase: http://purl.org/phylo/treebase/phylows/study/TB2:S30909) comprises sequences for 328 taxa (including all outgroup taxa), with an aligned length of 2255 bp; 1560 bp for the ETS, and 695 bp for the ITS region. The BEAST Maximum Clade Credibility (MCC) tree for the full dataset including outgroups is presented in Figure S1 in the Supporting Information.

In the pruned tree (HAP clade only; Figs. 3, S2, S3), relationships within the HAP clade are congruent with previous phylogenies generated using the same markers, with well supported clades recovered as in Galbany-Casals et al. (2014), except for one clade (J), members of which are recovered in our tree in three different clades (Figs. 3, S3). Within the HAP clade, support is generally high for most relationships, although backbone relationships are unresolved amongst the major clades, most notably in Clade 2B' (Figs. 3, S3). This tree comprises 216 tips, 182 from southern Africa, representing 74.3% of southern African *Helichrysum* species.

Many well-supported subclades, comprising between 3 and 13 taxa, are recovered in both our tree and the target-capture based trees of Blanco-Gavaldà et al. (2023). In this study, we present a gene tree representing the relationships recovered by the ribosomal DNA cistron, which has previously been found to correspond well with morphological and biogeographic patterns in the HAP lineage.

Our dating analysis places the root of subfamily Asteroideae in the Palaeocene (c. 63 Ma; median ages reported; epochs according to GSA v.6.0; Walker and Geissman, 2022), with confidence intervals stretching from the Cretaceous to the mid-Eocene (Table 2; Figure S1). While this estimate is consistent with the older age estimates for the Asteraceae (Barreda et al., 2015), our sampling outside of the HAP clade is sparse, and these estimates will be influenced by low species coverage. We estimate a mid-Eocene age (c. 46.55 Ma) for the ancestor of the Gnaphalieae, with confidence intervals from the very early Oligocene to the Palaeocene, and most divergence events within subtribe Gnaphaliinae very likely occurring in the Miocene (Figure S1). The HAP clade, however, represents one of the earliest radiations in the tribe, in the late Oligocene to Early Miocene [c. 25.5 Ma (35.1–17.7 Ma); Table 2; see Figures S1, S2].

3.2. Biogeographic analysis

Most ancestral nodes could be unequivocally and uniquely optimised to a single ancestral area, or to a composite of just two or three areas. Of the 212 nodes in the tree, 138 (65%) had a single highest probability for an ancestral area comprising just one or a few regions. For the remaining 73 nodes (35%), no ancestral area or composite of a few areas received a single highest probability, so we used cumulative probabilities to locate the ancestor in one or a few of our regions. The S-DEC output and calculations of cumulative probabilities are provided in Table S3 (see Supporting Information), and the most likely ancestral areas are mapped onto the tree (inferred across 1000 trees) in Figs. 3 and S3.

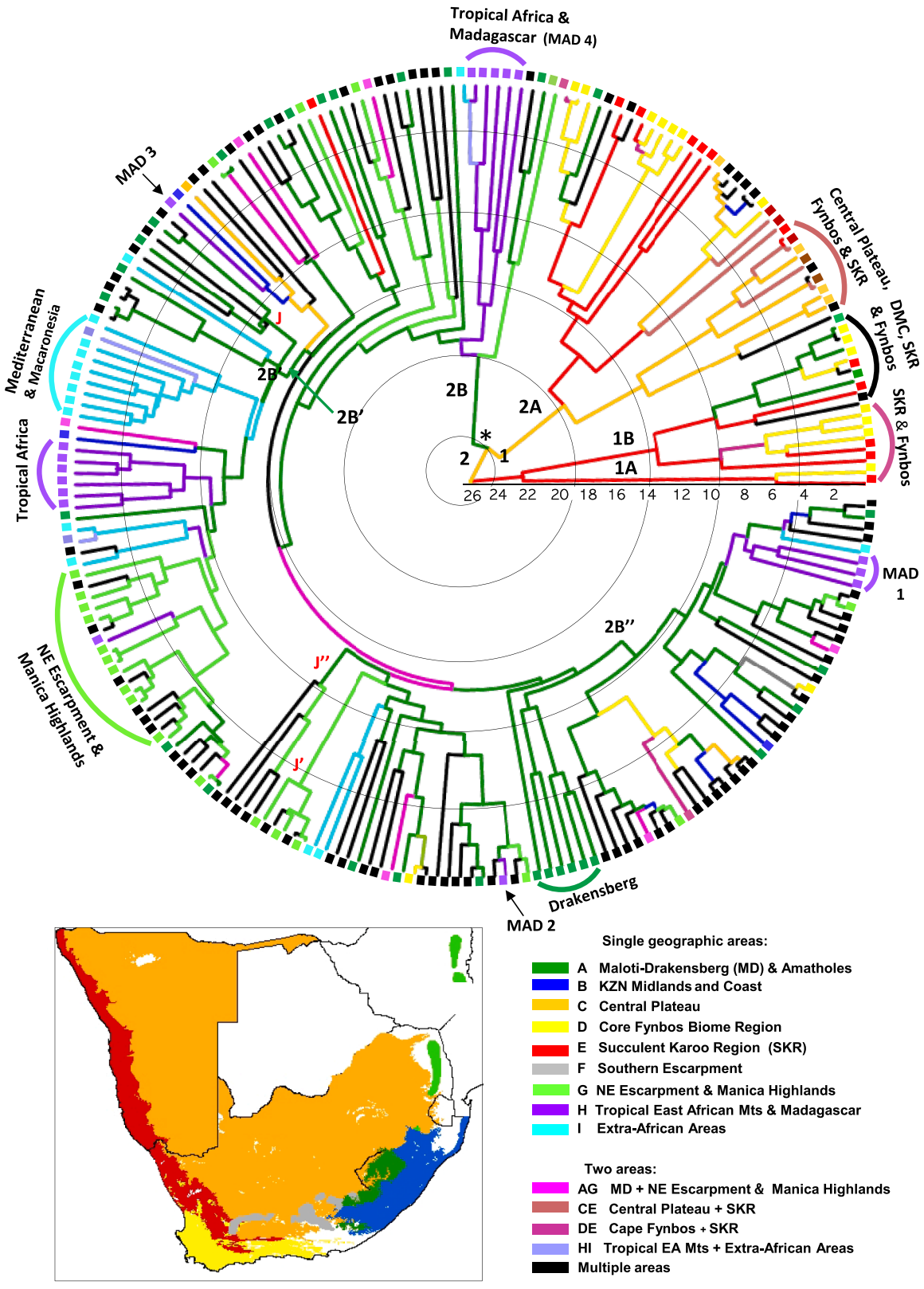

Fig. 3. Biogeographic history of African *Helichrysum* reconstructed using the DEC model on the time-calibrated BEAST MCC tree. Geographic areas are colour-coded on the branches according to the legend and as indicated on the map of southern Africa. Additional colours are used for branches where the highest probability of occurrence is assigned to one or a combination of two areas (see Legend). Lineages inferred to have occurred in three or more areas are coloured black.

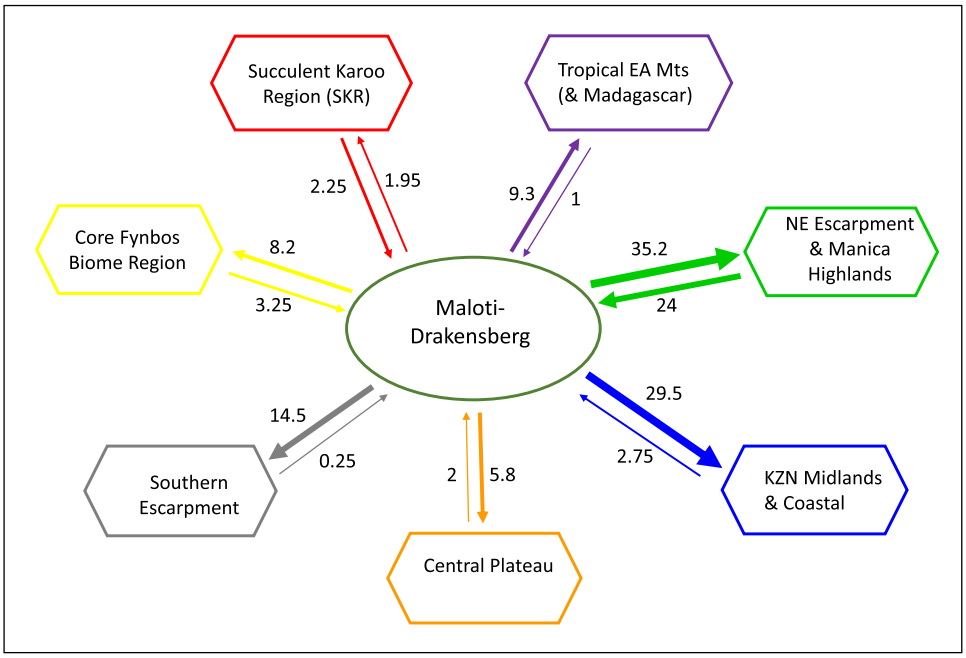

Fig. 4. Graphical summary showing number of dispersal events between the Maloti- Drakensberg and the other designated geographic areas within Africa, obtained from the SDEC analysis in RASP.

3.2.1. Origin and diversification of the HAP Clade

Our results infer an origin for the HAP clade in a composite area that includes the SKR and the Central Plateau of southern Africa (99.4% single highest probability) in the late Oligocene to early Miocene (c. 25.5 Ma; Figs. 3, S2). The early divergences within the HAP clade appear to have occurred during the late Oligocene to early Miocene (ca. 25.5–22.5 Ma, Figs. 3, S2).

The initial divergence gave rise to two lineages, the first of these (clade 1, the ancestor of clades 1A and 1B; Figs. 3, S3) subsequently diversified mainly in the arid SKR and the core Fynbos Biome region, with a direct migration from the SKR to the Maloti-Drakensberg grasslands in clade 1B (ca. 9 Ma) and limited speciation giving rise to at least three Drakensberg endemics, two of them alpine. Within this clade there is a second lineage (clade 2) that is inferred to have originated in the Central Plateau and given rise to a lineage (clade 2A) that diversified mainly in this region and in the SKR and core Fynbos Biome region, with a single dispersal to the Maloti-Drakensberg (c. 4.5 Ma, *H. lineatum*). The lineage clade 2B, arising from an ancestor in the Central Plateau, is inferred to have migrated directly to the Maloti-Drakensberg. This represents the earliest occupation of the Maloti-Drakensberg by HAP clade members, dated to the Early Miocene (24–18 Ma; ancestor at node *, Figs. 3, S2, S3).

Subsequent divergences leading to the various subclades in clade 2B appear to have occurred rapidly within a short space of time in the Mid-Miocene, resulting in a poorly resolved backbone (Figs. 3, S3). An extended ancestral presence in the Maloti-Drakensberg is evident in clade 2B; these ancestors giving rise to much of the species diversity of the HAP clade. Dispersals inferred to have taken place from out of the Maloti-Drakensberg in the Mid to Late Miocene resulted in *Helichrysum* lineages occupying a wide range of areas in the NE Escarpment, Tropical African mountains, and Madagascar over the period c. 17–13 Ma, as well as other regions within southern Africa (Figs. 3 and 4, S2, S3). Although rare, re-colonisations of the SKR (e.g. *H. excisum* [**]), Central Plateau (e.g. lineage leading to *H. tomentosulum* [***]), and the core Fynbos Biome region (e.g. *H. retortum*) are all inferred from Maloti-Drakensberg ancestors (see Figs. 3, S3).

3.2.2. Dispersals within Africa – a major driver of diversification in the HAP clade

Overall, dispersal is inferred to have played a much larger role in diversification of the HAP clade than vicariance (294 vs. 44 events respectively; Fig. 4, Table S4 in Supporting Information), with very little extinction (4 events). Our reconstruction suggests that two areas have predominantly functioned as sinks for successful colonisation from the Maloti-Drakensberg, viz., the NE Escarpment (35.2 dispersals) and the KZN Midlands and Coastal grasslands (29.5). A substantial number of dispersals are also inferred southwards from the Maloti-Drakensberg to the Southern Escarpment (14.5); fewer directly to the core Fynbos Biome region (8.2) and to the summer rainfall grasslands of the Central Plateau (5.8), with only two dispersal events inferred to the SKR (Fig. 4, Table S4).

At least nine dispersals are hypothesised here to have occurred from the Maloti-Drakensberg to the Tropical East African mountains, including some to Madagascar via these tropical mountains, for example, the *H. ibityense–H. xylocladum* clade 'MAD4' and the *H. triplinerve/Humeocline* clade 'MAD1', (Figs. 4, S2, S3). Our dating places the timing of the dispersals to the Tropical East African mountains during the Late Miocene, with diversification during the Pliocene and Pleistocene, resulting in a montane-alpine endemic/near-endemic clade that includes *H. brownei* and *H. stuhlmannii*, amongst others (Figs. 3, S3).

The other region that has served as a major source of dispersals (44 events) to other areas is the NE Escarpment (Fig. 4, Table S4), with the Maloti-Drakensberg and KZN Midlands and/or the Coastal grasslands being the main destinations (Fig. 4; Table S4). Dispersals from or via the NE Escarpment to the Tropical East African mountains occurred in the Late Miocene to Pliocene (e.g. *H. flammeiceps;* Figs. 3, S2). Dispersals to Madagascar occurred from the Mid to Late Miocene and during the Pliocene, including one that appears to have occurred directly from the Maloti-Drakensberg (*H. plantago*, ~1.5 Ma; 'MAD2') and another from Maputaland in northern coastal KZN (B) (*H. platycephalum*, ~8 Ma; 'MAD3', Figs. 3, S2). The earliest dispersal to Madagascar from the Tropical East African mountains is inferred here to have occurred in the Late-Miocene (c. 10.7 Ma) and to have resulted in a Madagascan diversification, giving rise to the clade ('MAD4') containing *H. ibityense* and *H. xylocladum*, whereas the *H. triplinerve - Humeocline* clade

('MAD1') ostensibly arose in the Late Miocene to Pliocene (Figs. 3, S2).

3.2.3. Out of Africa

At least six independent dispersals took place to regions outside of Africa in the HAP clade (Fig. 3; Table S4). While two of these evidently occurred from the geographically most proximate Tropical East African mountains, the remainder are inferred to have been long-distance dispersal from ancestors in the Maloti-Drakensberg region, although these nodes are poorly supported. These include dispersals northwards to the Mediterranean and Macaronesian regions in the Late Miocene (~11 Ma; in clade 2B'). The subsequent Mediterranean radiation includes the type species, *Helichrysum orientale* (Figs. 3, S2, S3). These series of divergence events from the ancestors of clades 2B'' and 2B''', are all inferred here to have occurred in the Maloti-Drakensberg, with subsequent independent colonisation of almost every other biogeographic region (Figs. 3, S2, S3).

Our phylogeny also suggests that dispersals could have occurred directly from ancestors in the Maloti-Drakensberg to the Mediterranean and Macaronesian regions in the Early Pliocene to Pleistocene (e.g., Mediterranean *H. serotinum* subsp. *picardi*, ~3.5 Ma; Macaronesia, *H. nicolai* Cape Verde; ~1.6 Ma), to South America (*Achyrocline,* ~5.6 Ma), and to far eastern Russia, Japan and North America (*Anaphalis*, ~10.6 Ma; Figs. 3, S2). *Pseudognaphalium* appears to have radiated in the Americas following dispersal from the NE Escarpment of South Africa via the mountains of East Africa in the Late Miocene (~7 Ma; Figs. 3, S2).

3.2.4. Dispersals into the Maloti-Drakensberg

Far fewer dispersals (35.6) are inferred to have occurred *into* the Maloti-Drakensberg region, with most of these (24 or 67%) from the NE Escarpment. Some of these dispersals to the Maloti-Drakensberg are back-migrations from lineages seeded by earlier outwards dispersals, largely also involving the North-Eastern Escarpment (12.5), but only one from the mountains of East and Central Africa. Very few dispersal events into the Maloti-Drakensberg are inferred to have originated from the Cape Fynbos Region, the SKR, or the Southern Escarpment (Fig. 4; Table S4).

3.2.5. In situ speciation in the Maloti-Drakensberg and other African regions

The 93 Maloti-Drakensberg *Helichrysum* species included here (of a total 102) occur in at least 35 different clades. Considerable speciation has therefore occurred within the Maloti-Drakensberg occurred (at least 79 events, Table S3). However, only one small clade of endemic taxa (*H. milfordiae, H. flanaganii, H. bellum, H. paleatum, H. evansii*) is evident in the present sampling (Fig. S3). Nonetheless, 12 clades include at least one Maloti-Drakensberg endemic species (e.g., *H. witbergense, H. marginatum, H. glaciale, H. lineatum*), and five additional clades have at least one near-endemic species. Substantial speciation has also occurred in the NE Escarpment (Figs. 3, S3; Table S4), resulting in a clade comprising taxa predominantly endemic to this region, e.g., *H. summomontanum, H. mariepscopicum, H. wilmsii; H. milleri*, and *H. albilanatum* (Figs. 3, S3).

The extent of diversification in *Helichrysum* occurring within the KZN Midlands & Coastal grasslands, Central Plateau, core Fynbos Biome region, and SKR ranges from 13–16 events per lineage (Table S4). The Great Winterberg-Amathole mountains (GWA, sensu Clark et al., 2014) share a significant number (41 of 84 species, 49%) of *Helichrysum* species with the Maloti-Drakensberg, of these, 15 species are shared with other Southern Escarpment mountains. A modest number of diversification events (15) is indicated for the Tropical East African mountains and Madagascar, but our reduced sampling of taxa from these regions renders this a significant under-estimate.

4. Discussion

Our phylogenetic and biogeographic analyses of the HAP clade focus on exploring patterns of floristic diversification within the southern African region, especially the role of the Great Escarpment, including the Maloti-Drakensberg, using the large, diverse genus, *Helichrysum*. This study, with a finer area definition in South Africa, complements those of Blanco-Gavaldà et al. (2023, 2025a, 2025b) which explore the biogeographic roles of the afromontane archipelago and the afroalpine region of Tropical Africa, ecologically driven patterns of diversification within Madagascar, and diversification patterns in mountains worldwide, respectively.

There are differences in topology between our Bayesian MCC tree and both the ML concatenation and summary coalescent (ASTRAL) trees of Blanco-Gavaldà et al. (2023, 2025a, 2025b), particularly in the relationships amongst the subclades. However, none of the HAP clade trees generated to date (based on either target enrichment, plastid, or ribosomal DNA) have been able to fully and with good support resolve all the backbone nodes in the HAP tree (e.g. Nie et al., 2016, Smissen et al., 2020: Blanco-Gavaldà et al., 2023, 2025b). Even the HAP clade trees based on the same target enrichment dataset analysed with contrasting approaches (i.e., summary coalescent [ASTRAL] versus concatenated ML approaches; Blanco-Gavaldà et al., 2023, 2025a, 2025b) exhibit some topological differences, possibly indicating inter-gene tree discordance. Allopolyploidy has been inferred for several lineages in the HAP clade, and efforts should be made to further identify taxa, lineages or genes which are particularly affected, and to account for these processes in phylogenetic analyses. In addition, our dates are somewhat earlier than Blanco-Gavaldà et al. (2025a) dates in the Pliocene and Pleistocene.

4.1. Origins, dispersal, and migration routes of Helichrysum in southern Africa

Comparison of our inferred ancestral area of the HAP clade to the slightly different biogeographic areas reconstructed by Blanco-Gavaldà et al. (2023, 2025a, 2025b) indicate that the ancestral area is most likely to be the SKR in the south-western Cape. This is also consistent with biogeographic reconstructions by Andrés-Sánchez et al. (2019), who inferred an origin for these lineages in the GCFR, an amalgamation of the CFR with the Succulent Karoo Biome region. Both our analyses and those of Blanco-Gavaldà et al. (2023) distinguish between the CFR and the SKR, allowing us to pinpoint the SKR as the likely area of origin. However, we date this origin to the Late Oligocene/Early Miocene, suggesting that the clade is part of the 'Desert I' floristic radiation of Linder & Verboom (2015).

This 'Desert 1' radiation is associated with the onset of summer aridity linked to development and strengthening of the Benguela Upwelling System in the Early to Mid-Miocene, respectively, linked to the opening of the Drake Passage, expansion of the Antarctic ice sheet, and cooling of the Southern Ocean (McCarthy and Rubidge, 2005; Senut et al., 2009; Pickford et al., 2014). The establishment of a rainfall gradient from east to west coasts resulted in hyper-aridity of the west coast of southern Africa (McCarthy and Rubidge, 2005), notably the Namib Desert (Senut et al., 2009; Pickford et al., 2014), and the Nama and Succulent Karoo regions. The arid conditions in the west were further exacerbated by uplift that started ca. 20 Ma, with the eastern portion of the continent rising more than the west (250 vs. 150 m), intensifying the east-to-west rainfall gradient (McCarthy and Rubidge, 2005).

The ancestor of the HAP clade must therefore have been adapted to an arid environment, possibly morphologically either like the extant small, annual species in the SKR, or the compact, mat-forming perennials with deep tap roots well adapted to desert-like conditions (Hilliard, 1983). The recent paper by Blanco-Gavaldà et al. (2025b) inferred the HAP clade ancestor to be a phanerophyte adapted to sandy soils. An

ecological shift to a cooler, moister montane grassland in a summer rainfall system is evident in the perennial lineages arising in the large, diverse *Helichrysum* clade with its ancestor in the Maloti-Drakensberg. The short, cool growing season characterising both habitats may be the basis of the ecological link. A similar pattern is seen in *Monsonia* L. (Geraniaceae), which also originated in the Early Miocene during the period of aridification of south-western Africa, diversifying into two main lineages, one comprising Namib Karoo succulents, and the other, perennial herbs of the Maloti-Drakensberg (García-Aloy et al., 2017).

Very few direct migrations are inferred between the more arid winter-rainfall regions of South Africa (the GCFR) and the mesic, summer-rainfall Maloti-Drakensberg. Only two species are inferred to have migrated back to the GCFR, one to the SKR (*H. excisum*) and one to the core Fynbos Biome region (*H. patulum*). Paucity of direct migrations between these regions may be because of differences in rainfall regime, with the GCFR experiencing winter rainfall vs. summer rainfall in the Maloti-Drakensberg. Differences in substrate are less likely to be the reason. Despite the nutrient poor Table Mountain Sandstones (TMS) of the CFR mountains being very different from the purportedly nutrient rich basalts of the alpine region of the Maloti-Drakensberg, the very low mineralization rates of these basalt-derived soils at high altitude (and low temperature) make them functionally equally nutrient poor (Carbutt et al., 2013, Carbutt and Edwards, 2015). The Stormberg Group 'Clarens' sandstone-derived soils at lower altitudes are intrinsically and functionally nutrient poor, like the TMS of the CFR. In addition, many species of *Helichrysum* appear well-adapted to the nutrient-poor quartzites of the mountains to the north of the Maloti-Drakensberg (Wild, 1964; Van Wyk and Smith, 2001).

There is no indication in our analysis that the Cape Fold Mountains and the Southern Escarpment acted as a stepping stone between the western SKR lineage and the Maloti-Drakensberg. Instead, lineages are inferred to have migrated via the Central Plateau or very rarely directly from the core Fynbos Biome region to the Maloti-Drakensberg. The route via the Central Plateau may have been facilitated by westward expansion of the cold-temperate climate over the Central Plateau during glacial maxima (see Fig. 1b in Taylor et al., 2024), possibly leading to interdigitation of arid and cold habitats, providing opportunities for evolution of cold-tolerance in the ancestors of the colonists. Similar selective regimes between semi-arid and cold temperate habitats may include a short growing season or the need for persistence strategies, such as periods of physiological inactivity, and/or increased longevity (Rosbakh and Poschlod, 2021). Thus, although floristic linkages between the Maloti-Drakensberg and the Southern Escarpment are evident in widespread species such as *H. albobrunneum, H. montanum, H. sessile*, and *H. trilineatum* (Hilliard, 1983), the southern section of the Great Escarpment appears not to have served as a major migration route for *Helichrysum* between the GCFR and the Maloti-Drakensberg, as proposed by Clark et al. (2012). This despite 8.8% of the Sneeuberg Mountain Complex's flora comprising Drakensberg near-endemics in other genera (Clark et al., 2009).

The section of the Southern Great Escarpment comprised by the Sneeuberg Mountain Complex transitions from an arid climate and arid-adapted vegetation in the west to the moister eastern mountains with their mesic montane grasslands (Van der Walt, 1980; Clark et al., 2011). In addition, physical barriers to migration exist in the form of the Fish River Interval (i.e. the Great Fish River Valley) that separates the arc of mountains known as the 'Sneeuberg' from the eastern Great Escarpment (Phillipson, 1987; Clark et al., 2009). This creates a barrier to migration eastwards to the Great Winterberg and Amathole mountains (GWA) and thence northwards to the Maloti-Drakensberg. A montane "bridge" does provide a route around the north of the Great Fish River basin linking the Sneeuberg to the Stormberg (Clark et al., 2009) but there is no evidence of this being used as a migration route in *Helichrysum*.

In this analysis, the Amathole endemic *H. isolepis* is located near the base of the clade wherein the bulk of diversification in the Maloti-Drakensberg occurs (Fig. S3, clade 2B), as well as diversification in other temperate and/or montane regions, including the mountains of Tropical Africa and Madagascar. In the phylogeny of Blanco-Gavaldà et al. (2025a), both *H. isolepis* and the Katberg (GW) endemic *H. montiscati* are similarly sister to the larger 'Grassland' clade members, including both Drakensberg and widespread species. However, two Drakensberg endemic species, *H. glaciale* and *H. bellidiastrum*, are placed sister to this large clade (Blanco-Gavaldà et al., 2025a). This suggests that species may have migrated southwards from the Maloti-Drakensberg to the Amathole, Great Winterberg and Katberg mountains. Either way, considerable exchange of species has occurred between these mountain regions.

Many more migrations apparently occurred southwards from the Maloti-Drakensberg to the GWA and Sneeuberg than in a northerly direction. However, the Southern Escarpment does not provide an uninterrupted southerly migratory route from the Maloti Drakensberg to the core Fynbos Biome region due to the Karoo Interval, which separates the Sneeuberg from the Cape Fold mountains in the south, and the Nelspoort Interval that divides it from the Nuweveldberg in the west (Clark et al., 2009). This is reflected in the Sneeuberg being the most western limit for most of the 102 Drakensberg near-endemics, while only ten species (0.8% of the Sneeuberg's flora) represent disjunctions across the Karoo Interval from the CFR to the Sneeuberg (Clark et al., 2009). This break in migratory route is also evident in distribution patterns of widespread species such as *H. albobrunneum, H. montanum, H. sessile*, and *H. trilineatum*, all of which appear to have originated in the Maloti-Drakensberg but do not extend westwards to the CFR (Hilliard, 1983).

4.2. Diversification of Helichrysum in southern Africa

The grasslands of southern Africa are likely to have developed during the late Miocene, together with the Nama-Karoo and Fynbos regions (Scott et al., 1997, Linder, 2003, Mucina et al., 2006), coinciding with the cooling of global ocean temperatures. The east-west temperature and moisture gradient over the sub-continent very likely determined the extent of grassland; enhanced by the second period of uplift during the Pliocene (Mucina et al., 2006). Our results place most of the earlier divergences in *Helichrysum* during the Late Miocene in the grasslands of southern Africa, including in the Maloti-Drakensberg and NE Escarpment, followed by a surge of divergences in the Pliocene and Pleistocene epochs.

Strong floristic links are evident between the Maloti-Drakensberg and the NE Escarpment in South Africa, with the LMEE and Manica Highlands both recognised centres of diversity (Clark et al., 2022). The largest number of migration events inferred here are between these two regions, followed by the KZN Midlands and Coastal region, also shown to be a major recipient of dispersals from the Maloti-Drakensberg, but with very few in return. Species occurring in both the montane zones of the Maloti-Drakensberg, the KZN Midlands and the low-lying coastal regions of KZN (Hilliard, 1983) suggest migration to the coast (*H. natalitium*), as well as occasionally from it (*H. auriceps*). This is in agreement with results shown by Blanco-Gavaldà et al. (2025a) globally for the HAP clade, a study that highlights the importance of montane habitats as a source of lowland lineages, especially in temperate latitudes.

The periods of greatest diversification of *Helichrysum* in southern Africa in general and in the Maloti-Drakensberg in particular coincide with the two periods of uplift linked to the expansion of grasslands in the broader region. These were centred in the KZN Midlands; the first, in the Late Miocene, resulted in an elevation increase of ca. 300 m, while the second resulted in uplift of as much as 900 m near the end of the Pliocene (Partridge and Maud, 1987; Partridge and Maud, 2000; McCarthy and Rubidge, 2005). The increased elevation of the Maloti-Drakensberg very likely resulted in alpine conditions at the summit (Partridge, 1998), and the uplift augmented the topographical heterogeneity in the Maloti-Drakensberg, creating opportunities for allopatric speciation and

adaptation to specific microclimates, e.g., *Craterocapsa* Hilliard & B.L. Burtt (Campanulaceae; Uys and Cron, 2013); *Arrowsmithia* DC. (formerly *Macowania* Oliv., Asteraceae, Bentley et al., 2014); *Killickia* Bräuchler, Heubl & Doroszenko (Lamiaceae; Kgaboesele, 2019). These dates also correspond with the origins of the endemic alpine Maloti-Drakensberg *Helichrysum* species, for example, *H. milfordiae* and *H. lineatum* in the Miocene to Pliocene, while others arose in the Pleistocene (e.g., *H. witbergense, H. nimbicola, H. praecurrens*) — most from ancestors within the Maloti-Drakensberg.

In addition, at least 12 *Helichrysum* colonizations have occurred from the mountains of southern Africa (including the Maloti-Drakensberg) to the montane zones of the Tropical East African mountains (Blanco-Gavaldà et al., 2023). Two of these were possibly directly from the Maloti-Drakensberg and one from the North-Eastern Escarpment (this study). At least three *Helichrysum* lineages reached the alpine belt in the Central and East African mountains and diversified *in situ* (Blanco-Gavaldà et al., 2023), however, only a few are strictly endemic afro-alpine species. Similarly, in *Senecio sensu stricto,* between four and 14 colonization events have occurred from southern Africa to the Tropical East African mountains, but there is no single large alpine radiation (Kandziora et al., 2016).

Dispersal has played a much larger role in *Helichrysum's* evolutionary history than vicariance (also see Blanco-Gavaldà et al., 2023), as is the case for most African mountain floras (Hedberg, 1970; Popp et al., 2008; Gehrke and Linder, 2009; Wondimu et al., 2014; Gizaw et al., 2016). Long distance dispersal has been inferred to explain the distribution of many taxa occurring in the high mountains of East Africa and along the Afromontane backbone of mountains (e.g., Gehrke and Linder, 2009; Gizaw et al., 2016; Brochmann et al., 2021; Blanco-Gavaldà et al., 2023). It is also key to explaining the distribution of *Helichrysum* across the mountains of Africa, with wind a likely the dispersal agent, given the small size of the cypselae of *Helichrysum* species (e.g., Hedberg, 1970), although the pappus is often soon caducous in *Helichrysum* and unlikely to play an important role in its dispersion.

These high elevation habitats in tropical Africa are very recent – a key reason for the prevalence of dispersal in the history of the 'afromontane' and 'afroalpine' floras. The earliest dispersal of *Helichrysum* into the highlands of East Africa in the Mid to Late Miocene coincides with the presence of an afro-alpine-like vegetation in Tropical Africa (Axelrod and Raven, 1978; Coetzee, 1967; Harmsen et al., 1991). Most of the species evidently migrated to montane environments initially, later diversifying or migrating into the alpine zone (Blanco-Gavaldà et al., 2023). Although the Ruwenzoris (an upthrust mountain) may have supported montane vegetation in the Mid- to Late Miocene (ca. 12 Ma; McConnell, 1959; Whittow, 1966), most of the volcanic East African mountains with alpine floras are estimated to have arisen in the Pliocene and Pleistocene epochs (Cahen et al., 1984), including Mt Kenya (3.5–2.0 Ma; Evernden and Curtis, 1965; Bagdasaryan et al., 1973) and Mt Kilimanjaro (1.1–0.23 Ma; Evernden and Curtis, 1965; Evans et al., 1971).

Long distance dispersal also occurred to Madagascar — already in or near its current position relative to Africa during the Late Miocene and Pliocene, when *Helichrysum* is hypothesised to have dispersed to the continental fragment island. Although the wind direction and ocean currents were no longer conducive to oceanic dispersal from Africa to Madagascar in the Mid-Miocene, more dispersal events are inferred for vertebrates, especially volant ones, after the shift in ocean water surface flow than before (Samonds et al., 2012). The most likely modes of trans-oceanic dispersal for plants' fruits and seeds (including the anemochorous ones) are via floating mats of vegetation or via birds or bats. However, the southwest Indian Ocean region is affected by cyclones and large tropical storms in the austral summer (Mavume et al., 2009; Ash and Matyas, 2010), and cyclones could certainly have dispersed seeds and fruits, such as the small cypselas of *Helichrysum*, from Africa to Madagascar (Samonds et al., 2012).

Our study hypothesises at least one dispersal event occurring directly from the Maloti-Drakensberg to Madagascar (*H. plantago*), and another (*H. platycephalum*) from Maputaland (northern coastal KZN). However, the main source of dispersals to Madagascar has been from Tropical Africa (Blanco-Gavaldà et al., 2023, 2025b). We also recovered putative migrations to the Americas, Asia, Macaronesia, and the Mediterranean region from within the large 'Maloti-Drakensberg clade'; the Maloti-Drakensberg therefore could have played a role in the world-wide HAP clade diversification over the last c. 18 million years. However, it is probable that Mediterranean *Helichrysum* species and *Anaphalis* migrated from Tropical Africa, possibly also the American *Pseudognaphalium* and *Achyrocline* (Blanco-Gavaldà et al., 2023). This is difficult to precisely assess due to the limitations of the methods applied for phylogenetic reconstruction in inferring origins and relationships of groups of allopolyploid origins, such as these ones (Smissen et al., 2011).

4.3. The Maloti-Drakensberg as a 'melting pot' and 'stepping stone' along the Afromontane archipelago

Use of the Maloti-Drakensberg as a steppingstone northward to the East African mountains has been inferred for three Cape-centred genera, *Disa* P.J.Bergius (Orchidaceae), *Pentaschistis* Stapf. (Poaceae), and *Moraea* Mill. (Iridaceae; Galley et al., 2007). However, these hypotheses need to be tested via ancestral biogeographic reconstructions using species-level phylogenies. In a phylogenetic/biogeographic analysis of *Erica* Tourn. ex L., Pirie et al. (2019), however, found no migration southwards from the mountains of Central Africa to the Cape via the Maloti-Drakensberg, but rather that the Maloti-Drakensberg served as a 'melting pot' for diversification in the genus.

Most dispersals to the Maloti-Drakensberg have been from the NE Escarpment, whereas very few arrivals from the southern regions (core Fynbos Biome region and SKR) have occurred, including from or via the Southern Escarpment. This suggests that for *Helichrysum*, the Maloti-Drakensberg has only occasionally served as a 'stepping stone' from its origin in the SKR for migration northwards along the Afromontane archipelago (also see Blanco-Gavaldà et al., 2023). This is evident mainly at genus level, as widespread *Helichrysum* species appear not to have originated in the Cape and migrated via the Maloti-Drakensberg.

Instead, the ancestors of four very widespread *Helichrysum* species (*H. herbaceum, H. mundtii, H. nudifolium var. nudifolium* and *H. odoratissimum*) all appear to have arisen in the Maloti-Drakensberg and migrated northwards along the Afromontane archipelago to the tropical high mountains of East Africa as well as southwards to the GCFR — based on their current distributions (Hilliard, 1983; NewPOSA; Flora of Zimbabwe Website, Beentje, 2002; Table S3). Similarly, the ancestors of the widespread species *H. splendidum, H. subglomeratum*, and *H. umbraculigerum* appear to have originated in the Drakensberg, migrating northwards to the Manica Highlands and southwards along the Southern Great Escarpment. However, these hypotheses need to be confirmed with a complete sampling of the genus and population-level sampling of these widespread species.

4.4. In situ diversification in the Drakensberg

Extensive speciation in *Helichrysum* has occurred within the Maloti-Drakensberg, but no single large radiation, similar to *Moraea* (Iridaceae; Goldblatt et al., 2002). In contrast, in the large orchid genus *Disa*, considerable speciation has occurred from three migrations into the Maloti-Drakensberg from the Cape (Bytebier et al., 2006; Galley et al., 2007). Furthermore, very little speciation in *Helichrysum* has occurred in the alpine zone of the Maloti-Drakensberg, where frost and snow frequently occur (Grab, 2013; Grab et al., 2017). Only seven species are strictly alpine (i.e. above 2800 m a.s.l.), although others extend into the alpine zone. A low speciation rate may be true of alpine-adapted plants in general, since the cold climate and exposure to wind and UV radiation require investment in persistence rather than reproduction, resulting in long generation times and presumably, slower rates of evolution and

migration (Forbis and Doak, 2024).

5. Conclusion

The grasslands of the Central Plateau, rather than the more arid Southern Escarpment, appear to have served as the main route for migration of species northwards from the CFR and SKR of southern Africa. Nonetheless, the eastern sections of the Great Escarpment, especially the Maloti-Drakensberg and the NE Escarpment, have played a fundamental role in the diversification of *Helichrysum* in southern Africa, which is likely true for other components of the temperate flora. This role is notable as a source for multiple dispersals into other cool growing-season biomes within the region, with some species reaching the high mountains of tropical East Africa and Ethiopia. The Maloti-Drakensberg and NE Escarpment may also have seeded dispersals outside of the African mainland, to Madagascar, the Mediterranean and Macaronesia, but confirmation of this requires further analyses accounting for the effects of allopolyploidy in phylogenetic reconstruction.

Figure S1_SuppInfo. BEAST MCC tree including all outgroups. Values at nodes indicate Bayesian posterior probabilities, with branches coloured according to level of PP support: ranging from blue [high] through dark green [low] to pale green [unresolved]. Fossil calibration nodes indicated by stars (*); secondary calibration nodes indicated by arrows. The circled node indicates the crown node of tribe Gnaphalieae.

Figure S2_SuppInfo. Pruned, dated tree based solely on the 270 HAP-clade sequences; blue branches = strong support, green branches = weak (unresolved).

Figure S3_SuppInfo. Pruned tree showing biogeographic history of *Helichrysum* and representative members of the HAP clade, with median dates above and Posterior Probabilities ($\geq$ 0.88) below the nodes. *'s = back-colonizations; J, J', J'' = clades not matching topology of phylogeny in Galbany-Casals et al. (2014; see text).

Table S1_SuppInfo. List of accessions/taxa included in this analysis – including species' names with authorities, voucher and locality information, and Genbank numbers.

Table S2_SuppInfo. Summary of aligned length of ETS and ITS regions, parsimony informative sites and percentage HAP clade taxa represented for each region/subregion of the alignment.

Table S3_SuppInfo. The S-DEC output from RASP and calculations of cumulative probabilities for areas.

Table_S4_SuppInfo (a) Total number of dispersal events occurring from and to the nine biogeographic areas coded for the SDEC analysis of the HAP clade in RASP as well as speciation within each area. (*Numbers for areas H and I are not an accurate reflection due to reduced sampling of clades in these areas.)

Table_S4_SuppInfo (b) Number of dispersals to and from biogeographic areas as indicated by the SDEC analysis of the HAP clade in RASP.

CRediT authorship contribution statement

Glynis V. Cron: Writing – original draft, Resources, Investigation, Formal analysis, Data curation, Conceptualization. **Mercè Galbany-Casals:** Writing – review & editing, Resources. **Santiago Andrés-Sánchez:** Writing – review & editing. **Marinda Koekemoer:** Writing – review & editing, Resources. **Nicola G. Bergh:** Formal analysis, Investigation, Methodology, Resources, Software, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The lead author is an Editorial Board Member/Editor-in-Chief/Associate Editor/Guest Editor for this journal and was not involved in the editorial review or the decision to publish this article.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.sajb.2025.08.007.

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