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1 Heathers (*Erica*; Ericaceae) of Madagascar: taxonomy, evolution, 2 ecology and uses

3

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14

15 Abstract

16

17 Madagascar is a regional diversity centre of the plant genus *Erica* L. (heathers; *anjavidy* in
18 Malagasy), with 35 species currently recognised. There is no modern taxonomic treatment of
19 the group, and many collections remain unidentified. We review the taxonomic history of
20 Malagasy *Erica*, built largely on the 1927 revision by Perrier de la Bâthie, who treated them
21 as *Philippia*. We summarise diagnostic species descriptions and incorporate them into the
22 *Erica* Identification Aid. There is clearly morphological variation that is poorly reflected in
23 current species concepts and requires further study. Malagasy *Erica* most likely form a
24 single radiation also encompassing species from the Mascarenes, according to published
25 and new phylogenetic data. However, resolution within the group is poor, and most species
26 remain unsequenced. Literature and specimen records show that *Erica* is found in all regions
27 of Madagascar except the dry west and southwest, with the highest species richness on the
28 high mountains. Habitats include the high-altitude “ericoid thickets”, shrubland–grassland
29 mosaics in the central highlands and on the eastern coast, and *Uapaca bojeri* (tapia)
30 savanna. The ecology of individual *Erica* species is insufficiently known. There may be both
31 wind- and (currently undocumented) insect-pollinated species. Many *Erica* species are likely
32 to be part of dynamic ecosystems with infrequent fire regimes. The paleorecord indicates a
33 more widespread ericoid shrub vegetation during the last glacial period. *Erica* is mainly used
34 as fuelwood, but local uses as tools and medicine have also been reported. None of the

35 Malagasy species has had its conservation status assessed, but estimates suggest at least
36 one-fifth of the species may be threatened. Taxonomic revision of the group, coupled with
37 phylogenomics, is an urgent priority. This would also enable better assessments of
38 ecological variation, local uses and conservation priorities.

39

40 **Keywords**

41

42 *anjavidy*, *Erica*, ericoid thicket, fire ecology, Madagascar, Mascarenes, *Philippia*, vegetation
43 history

44

45

46 **Introduction**

47

48 The huge plant genus *Erica* L. (heathers; Ericaceae) has one of its regional centres of
49 diversity in Madagascar. Currently, 35 species are accepted for the island, all endemic
50 (Antonelli et al. 2022, Elliott et al. 2024, World Flora Online 2024). *Erica* is one of three
51 Ericaceae genera in Madagascar along with *Agarista* D.Don ex G.Don, with seven species,
52 and *Vaccinium* L., with four species. Heathers and other Ericaceae are key to understanding
53 Malagasy vegetation dynamics: They form one of the main components of a high-mountain
54 vegetation type singled out as “Madagascar ericoid thickets”, with a globally distinctive and
55 endangered biodiversity (Crowley 2004, Dinerstein et al. 2017). They also occur in other
56 vegetation types especially in the central highlands of Madagascar, where the role of
57 humans and fire in shaping open habitats is debated (e.g. Joseph et al. 2021, Silander Jr. et
58 al. 2024). According to Phelps et al. (submitted), “the genus *Erica* is likely key to
59 understanding grassland–shrubland–savanna dynamics” in Madagascar. Yet there has not
60 been a taxonomic revision since that of Perrier de la Bâthie (1927). The genus and family
61 were not treated in two major reference works on the natural history of Madagascar
62 (Goodman & Benstead 2004, Goodman 2022), nor in the *Flore de Madagascar et des*
63 *Comores* series. Increasing our knowledge base on the taxonomy and ecology of Malagasy
64 *Erica* is thus a priority, both in the contexts of Madagascar’s highly endangered biodiversity
65 (Ralimanana et al. 2022) and the Global Conservation Consortium for *Erica* (Pirie et al.
66 2022). Here, we summarise existing data on *Erica* in Madagascar to identify knowledge gaps
67 and research priorities.

68

69 **Taxonomy**

70

71 Of the currently recognised Ericaceae genera in Madagascar, *Erica* (Ericoideae; Ericaceae) is
72 easily distinguished from *Agarista* and *Vaccinium* (both Vaccinioideae), most obviously by its
73 often needle- or scale-like leaves characterised by revolute margins almost touching on the
74 underside (“ericoid leaves”), arranged in whorls of 3-6, and its persistent corolla enveloping
75 the fruit (Oliver 2000, Schatz 2005). However, within *Erica* and the tribe Ericaceae, generic

76 bounds were a longstanding subject of debate that was only resolved towards the end of the
77 last century.

78 The current state of taxonomy in Malagasy *Erica* (morphological diversity shown in Fig. 1) is
79 largely founded on the work of Perrier de la Bâthie (1927b, 1934). His revision (Perrier de la
80 Bâthie 1927a) in particular already included descriptions of most of the species recognised
81 today, sixteen of which were new. Perrier treated them all under the African-Malagasy
82 genus *Philippia*, distinguished by small flowers with a zygomorphic calyx lacking, or resulting
83 from the fusion of, the subtending bracts typical of *Erica* in the strict sense. Both Perrier and
84 Alm and Fries, who published a monograph of *Philippia* earlier in the same year (Alm and
85 Fries 1927), wrote of inconsistency in the characters distinguishing genera in Ericaceae. The
86 latter erected a separate genus, *Mitrastylus* Alm & T.C.E.Fr., for two species with a
87 distinctive folded-back stigmatic disc (a structure somewhat resembling a broken umbrella
88 with rib-like lobes, in contrast to the expanded disc form more typical of wind-pollinated
89 *Erica*). Both species of *Mitrastylus* were from Madagascar: *E. parkeri* (Baker) Dorr &
90 E.G.H.Oliv. (Figure 1 G) and *E. madagascariensis* (H.Perrier) Dorr & E.G.H.Oliv. All the taxa
91 originally described under *Philippia* or treated under other genera in Ericaceae (including
92 *Mitrastylus*) were later transferred into *Erica* with new combinations and names by Dorr and
93 Oliver (1999). This followed Oliver (1987, 1988) whose work extended to including in a
94 broadly defined *Erica* all related so-called 'minor genera' (Nelson et al. 2024). After Perrier's
95 revision (1927), three additional Malagasy species and one subspecies were described: *Ph.*
96 *quadratiflora* H. Perrier (= *E. quadratiflora* (H. Perrier) Dorr & E.G.H. Oliv.) in Perrier de
97 Bathie (1930); *Erica marojejyensis* Dorr, *Erica bosseri* Dorr, and *Erica lecomtei* subsp.
98 *ravinakely* Dorr in Dorr & Oliver (1999). There has not been a more recent revision of the
99 group.

100 Perrier (1927a) grouped the Malagasy species according to morphological characters which
101 he ranked in order of importance. Most important was the shape of the stigma, on which
102 Perrier defined two sections: I (Cornigerae) for species with expanded stigmatic lobes

103 (including, but not limited to, the 'mitrastyulous' species; his numbers 1-7, Appendix 1); and II
104 (Discoidales) for those with a more typical discoid stigma (numbers 8-34). This was followed
105 in descending order of importance by the arrangement of the leaves (particularly in whorls of
106 three versus of four); indument (he distinguished four types differing e.g. by length and
107 presence or not of glands); leaf shape; inflorescence structure (terminal clusters of flowers,
108 or not); flower and style shape (particularly shape and relative size of sepals); and degree of
109 fusion of the stamens. Some species are distinct and easily identified even from images,
110 such as *E. perrieri* Dorr & E.G.H.Oliv. with its unique open-backed leaves (Fig. 1 H). Most of
111 the others are less obvious.

112 Perrier (1927a) noted the considerable variation given age, season, and conditions
113 (including the impact of fire), with particular emphasis on habit and on changes in (or loss of)
114 diagnostic characters after flowering. He also mooted hybridisation between species. His
115 concepts for some particularly variable species (such as *E. goudotiana* (Klotzsch) Dorr &
116 E.G.H. Oliv., treated as *Philippia cauliflora* Hochr.) deliberately focussed on the most
117 common form, with deviation from that form described separately. Dorr and Oliver (1999)
118 also indicated variation within species e.g. within *E. goudotiana*, for which they noted that
119 formal recognition 'awaits further study'. The numbers of specimens available for such study
120 appears to be small given the numbers of taxa involved, and a large proportion of that which
121 is documented in available archives remains unidentified (see below). The species were
122 included in earlier versions of the *Erica* Identification Aid (*Erica* ID aid; Oliver et al. 2024), but
123 the data was largely incomplete, preventing its effective use. There may be undescribed
124 variation within the current backlog of unidentified material. We need tools to facilitate
125 identifications of Malagasy *Erica* species, and more collections to better understand the
126 complex patterns of morphological variation in the group.

127 In this work we summarised information available from the literature to populate the ID aid.
128 Through work on the World Flora Online (WFO) Taxonomic Expert Network for Ericaceae
129 (Elliott et al., in prep.), we have made openly available the current state of knowledge of

130 *Erica* nomenclature (Elliott et al., 2024). A list of currently accepted Malagasy taxa with links
 131 to WFO and GBIF and diagnostic descriptions derived from Perrier (1927a) and Dorr and
 132 Oliver (1999) is presented in Appendix 1. We have incorporated these into an update of the
 133 *Erica* ID aid (current version: <https://doi.org/10.5281/zenodo.10407033>), including coding of
 134 characters used in the ID aid for narrowing down potential identifications.

135
 136 **Phylogenetics and evolution**

137
 138 Malagasy *Erica* form a single clade which also includes species from the Mascarenes (Fig.
 139 2), based on the available phylogenetic sampling. A single origin of the Malagasy *Erica* was
 140 already postulated by Perrier (1927a) and mirrors the numerous plant and animal radiations
 141 that occurred after dispersals to the island (Vences et al. 2009). Molecular phylogenetic
 142 studies based on regions from the chloroplast genome and nuclear ribosomal DNA
 143 (including the internal transcribed spacer region, ITS), have supported this Malagasy clade
 144 and shown it to be nested within a broader tropical African clade, which itself is sister to the
 145 large Cape radiation of *Erica* (Fig. 1a-b; Pirie et al. 2011, 2016, 2024). We here expanded
 146 the dataset of Pirie et al. (2024) with ITS data for additional collections from Madagascar and
 147 Mascarene islands, bringing the totals to 52 from Madagascar (including 13 identified
 148 species represented by 22 collections and 30 further collections unidentified to species), four
 149 from Mauritius (two collections each of both species), and five from La Réunion
 150 (representing all three species) (Table S1). We estimated a Maximum Likelihood phylogeny
 151 for the Malagasy clade and its sister group, using RAxML v.8 (Stamatakis 2014) and
 152 otherwise following the methods of Pirie et al. (2024). The results are presented in Fig. 2,
 153 along with those of Pirie et al. (2024).

154
 155 The topology presented by Pirie et al. (2024) showed several supported clades. *Erica*
 156 species from the Mascarenes, i.e. Mauritius (*E. brachyphylla* (Benth.) E.G.H.Oliv., *E.*
 157 *mauritiensis* E.G.H.Oliv.) and Réunion (*E. arborescens* (Willd.) E.G.H.Oliv., *E. galioides*

158 Lam., *E. reunionensis* E.G.H.Oliv.), form at least four separate lineages within the Malagasy
159 clade. This strongly suggests that *Erica* dispersed once from continental Africa to
160 Madagascar, diversified there and then further dispersed several times independently to the
161 Mascarenes. Neither *Erica comorensis* (Engl.) Dorr & E.G.H.Oliv. (Comoros archipelago) nor
162 *E. mafiensis* (Engl.) Dorr (Mafia island; off the Tanzanian coast) have yet been sequenced:
163 Whether these also belong to the Malagasy clade warrants testing.

164

165 The close relationship of *E. madagascariensis* and *E. humbertii* (H.Perrier) Dorr &
166 E.G.H.Oliv. might have been expected from Perrier's (1927a) revision, which grouped these
167 mitrastyulous species. However, *E. parkeri*, which also shares this trait, falls in a separate
168 clade with another (unidentified) mitrastyulous species plus *E. isaloensis* (H.Perrier) Dorr &
169 E.G.H.Oliv. and *E. boutonii*. Perrier placed the latter two in Sections I (Cornigerae) and II
170 (Discoidales) respectively, thus splitting them between the two major groupings defined by
171 stigma morphology. This warrants further investigation, suggesting that important diagnostic
172 characters potentially relating to pollination mode – including the mitrastyulous stigma – may
173 have evolved in parallel. Similarly, the clade including *E. perrieri*, *E. myriadenia* and *E.* 'cf.
174 *baroniana*' represents a wide range of Malagasy *Erica* variability, particularly of leaf shape
175 and indument type, and these species are correspondingly dispersed across Perrier's
176 system. The rapid radiation of Malagasy *Erica* was apparently accompanied by
177 morphological, and in particular, floral disparification, but whether this represents adaptive
178 variation remains to be tested.

179

180 The additional ITS data added to the existing supermatrix of plastid and ITS/ETS data of
181 Pirie et al. (2024) falls unambiguously within a monophyletic Malagasy/Mascarene clade, but
182 does not result in a well supported internal topology. Undetermined collections that we
183 tentatively grouped into morphospecies tended to show similar sequence variation (Fig. 2c),
184 but such variation was low and the groupings unsupported. This is in contrast to within the
185 *Erica* Cape clade, which represents an order of magnitude more species than the Malagasy

186 clade but nevertheless shows enough variation in ITS to be able to test the relationships of
 187 individual specimens (Hoekstra et al., in prep.). The difference in sequence variation may be
 188 explained by a combination of younger age and/or faster diversification rates of Malagasy
 189 lineages. *Erica* is estimated to have arrived in Madagascar around 5-7 million years ago on
 190 the basis of relaxed clock molecular dating and a secondary Ericaceae calibration (Pirie et
 191 al. 2016). From these results, Pirie et al. (2016) estimated that the Malagasy clade may have
 192 one of the highest diversification rates in *Erica*. Given the dependence of these estimates on
 193 both absolute time calibration and relaxed clock assumptions, they should be revisited with
 194 further, phylogenomic data and ideally more calibration points. This would also allow
 195 reconstructing trait evolution within the Malagasy clade and testing e.g. for parallel evolution
 196 of insect pollination from a probably wind-pollinated ancestor.

197

198 **Distribution and habitats**

199

200 We retrieved available georeferenced records for *Erica* and other Ericaceae from
 201 Madagascar via the Global Biodiversity Information Facility (GBIF.org, accessed 5
 202 November 2024, <https://doi.org/10.15468/dl.pmcvqr>). They were filtered using R and
 203 CoordinateCleaner (Zizka et al. 2019) to remove potentially spurious occurrences, including
 204 records with a reported precision >0.01° or 10 km and those with coordinates within 2 km of
 205 the country centroid, capital, or herbaria. This left 882 usable occurrences for *Erica*, 634 for
 206 *Agarista* and 872 for *Vaccinium*. Of the *Erica* occurrences, only 530 (60 %) were identified to
 207 species. Twenty-five records were reported as (endemic) South African species, however in
 208 each case the species includes a synonym with an epithet matching a Malagasy *Philippia*.
 209 This is unlikely to be a coincidence. In these cases we assumed that the name originated by
 210 erroneously applying a *Philippia* epithet under *Erica*, and corrected the name following Dorr
 211 & Oliver (1999): “*Erica aristata*” = *E. bojeri* Dorr & E.G.H.Oliv.; “*E. gracilis*” = *E.*
 212 *rakotozafyana* Dorr & E.G.H.Oliv.; “*E. hispida*” = *E. perhispida* Dorr & E.G.H.Oliv.; “*E.*
 213 *latifolia*” = *E. perrieri* Dorr & E.G.H.Oliv.; “*E. nudiflora*”, “*E. sparsa*” and “*E. trichoclada*” all =

214 *E baroniana* Dorr & E.G.H.Oliv. These cases highlight persisting confusion in the taxonomy
215 of Malagasy *Erica*.
216
217 *Erica* is found in all except the driest regions of Madagascar (Fig. 3). Plotting *Erica*
218 occurrences against Madagascar's ecosystems (Fig. 3a), following the map of Antonelli et al.
219 (2022), shows that *Erica* is found in all major ecosystem types except the western dry forests
220 and the southwestern spiny forest (and the coastal mangroves). This includes the
221 grassland–woodland mosaic of the central highlands, humid forest, and tapia savanna. Two
222 specimens only identified to genus suggest *Erica* may also occur in the Makay massif in
223 southwestern Madagascar, at the northern edge of the “subhumid forests” area. The “ericoid
224 thickets” (Crowley 2004), described in some vegetation classifications and defined by *Erica*
225 and similar “ericoid” shrubs, are confined to the four highest mountain massifs: Tsaratanana,
226 Marojejey, Ankaratra and Andringitra (Fig. 3b). According to other authors, vegetation of this
227 type also occurs further south, on the summit of Andohahela (Goodman et al. 2018c). The
228 ericoid thickets cover only c. 1,300 km² in total (Crowley 2004). The high mountains is also
229 where the species richness of *Erica* is highest, peaking in the Ankaratra and Andringitra
230 ranges, each with 13 species recorded per 0.5x0.5 ° grid cell (Fig. 3c). Six species appear to
231 be endemic to Andringitra alone (Appendix 1). Perrier (1927b) named *Philippia floribunda*
232 Benth. (= *Erica baroniana* Dorr & E.G.H. Oliv.) as the only species occurring at sea level in
233 Madagascar, but *E. goudotiana* and *E. leucoclada* have also been recorded from the
234 Eastern coast (Appendix 1, Fig. S1). The other two Ericaceae genera *Agarista* and
235 *Vaccinium* have distribution patterns broadly similar to *Erica* in Madagascar (Fig. 3d-f); they
236 have additionally been recorded from isolated humid forest areas of the western Bongolava
237 region, which suggests *Erica* might also occur there.
238
239 *Erica* species in Madagascar are open-habitat shrubs or form their own canopy (Perrier de la
240 Bâthie 1927b, Silander Jr. et al. 2024). Based on the literature, there appear to be three
241 main habitat types:

242

243 (1) *Ericoid thicket*. This high-altitude vegetation was singled out as a distinct type under
 244 different names in treatments of the Malagasy flora (listed in Gautier et al. 2018), including
 245 the global ecoregions of Dinerstein et al. (2017). A 2004 ecoregion assessment classified its
 246 biodiversity as “globally endangered” and assigned it a conservation status of “Endangered”
 247 (Crowley 2004). It was included in the “humid forests” by Moat and Smith (2007) and
 248 Antonelli et al. (2022). In the ericoid thicket, *Erica* is associated with other shrubs of similar,
 249 “ericoid” appearance, especially *Helichrysum* (Asteraceae) and *Vaccinium* (Koechlin 1972).
 250 Perrier (1927b) assumed this to be the original habitat of most *Erica* species in Madagascar,
 251 before it was supposedly destroyed by fire and *Erica* survived only in secondary vegetation.
 252 He also noted that *Erica* extends into the humid forest found in the zone below the ericoid
 253 belt, so the exact boundary between this vegetation type and the ericoid thicket is somewhat
 254 fuzzy. Among the high-altitude species, Perrier (1927b) cited three as specifically associated
 255 with the edges of marshes and bogs: *Philippia madagascariensis* and *Ph. pilosa* (both now
 256 synonyms of *Erica madagascariensis*), and *Ph. humbertii* (= *Erica humbertii*). Dorr & Oliver
 257 (1999) described *Erica bosseri*, confined to marshes in Ankaratra.

258

259 (2) *Grassland–shrubland mosaic*. This mixed vegetation type, difficult to classify (Antonelli et
 260 al. 2022), is found at lower altitudes, especially in the central highlands. The dominance of
 261 *Erica* shrubland versus grassland is probably dynamic and dependent on the fire regime
 262 (see below). In Ambohitantely Special Reserve in the centre, *Erica* forms part of the ecotone
 263 between grassland and forest (Ratsirarson et al. 2003). Perrier (1927b, 1927a) interpreted
 264 most of the *Erica* shrubland outside the high-altitude areas as secondary, anthropogenic
 265 vegetation resulting from forest destruction through fire (“*savoka à Philippia*”; *savoka*
 266 meaning fallow vegetation in Malagasy). The precise roles of fire regimes and land use in
 267 shaping the open vegetation of the central highlands are still debated (Joseph et al. 2021,
 268 Rakotoarivelo et al. 2024, Silander Jr. et al. 2024). In humid, high-altitude areas of
 269 Andringitra, the shrub-like, flammable grass *Panicum cupressifolium* appears to functionally

270 mimic *Erica* (Lehmann et al. 2022). In eastern Madagascar, *Erica* is found in coastal habitat
271 mosaics with grassland around littoral forest fragments. These open patches were also often
272 interpreted as secondary vegetation (e.g. in Manombo Special Reserve, Goodman et al.
273 2018b). However, a palaeoecological study of littoral forest fragments around Mandena
274 suggested that “ericoid grassland” with *Erica* and *Myrica* (Myricaceae) had already been part
275 of a dynamic landscape before the arrival of humans (Virah-Sawmy et al. 2009a). A
276 historical shift from forest to ericoid grassland around 1.400 cal. yr BP was attributed to the
277 effects of sea level rise and drought rather than human action (Virah-Sawmy et al. 2009b).

278

279 (3) *Tapia savanna*. This type of open-canopy vegetation, dominated by the tapia tree
280 (*Uapaca bojeri*, Phyllanthaceae), is found in several disjunct areas of the central highlands,
281 with its largest extent in Isalo (Fig. 3a). It is adapted to fire and distinct from forest but also
282 from the otherwise treeless grasslands of the central highlands (Kull 2002,
283 Solofondranohatra et al. 2018). *Erica* forms part of the tapia understory alongside *Vaccinium*
284 and other shrubs and smaller trees (Koechlin 1972, Gautier et al. 2018). *Erica danguyana*
285 (H.Perrier) Dorr & E.G.H.Oliv. and *E. jumellei* (H.Perrier) Dorr & E.G.H.Oliv. appear to be
286 specifically associated with tapia savanna in the centre around Antsirabe and Arivonimamo,
287 respectively; *Erica ibityensis* (H.Perrier) Dorr & E.G.H.Oliv., *E. lecomtei* (H.Perrier) Dorr &
288 E.G.H.Oliv. and *E. isaloensis* may also be tapia-associated, according to their distributions
289 on Mt. Ibity in the centre (the former two) and the Isalo sandstone massif in the southwest;
290 *Erica cryptoclada* (specifically the “var. *hybrida*” H.Perrier) was also found under tapia in
291 Isalo, in addition to high altitude ericoid thicket (Perrier de la Bâthie 1927b, Dorr and Oliver
292 1999). Tapia savanna is actively managed by the local population; while the cutting of tapia
293 trees is prohibited, *Erica* and other shrubs are extracted as fuelwood and for other uses (Kull
294 2002).

295

296 **Ecology and interactions**

297

298 Malagasy *Erica* appear to be adapted to fire. Perrier (1921, 1927b, 1927a) viewed most
299 open vegetation on Madagascar, including ericoid shrubland, as the result of degradation
300 through fire set by humans. Today, it is generally accepted that fire was already part of
301 Madagascar's landscape well before human arrival (Kull and Lehmann 2022), and modern
302 fire regimes are similar to those of other tropical regions (Phelps et al. 2022). *Erica* are
303 favoured by an infrequent fire regime: a study at Ambohitantely found *Erica* and Asteraceae
304 shrubs appearing on sites that had not burnt for seven years (Randriatsara 2014). In
305 Andringitra National Park, there has been a programme using fire to control *Erica* spread
306 into open grassland for conservation purposes (Rasolonandrasana and Grenfell 2003),
307 although a certain frequency of fire appears to favour *Erica* (Goodman et al. 2018a). At
308 higher fire frequencies, grasses will dominate; at lower frequencies, trees may colonise and
309 outcompete shrubs like *Erica* (Silander Jr. et al. 2024). It is likely that *Erica* in the central
310 highlands historically formed part of a spatially shifting, decadal to centennial vegetation
311 dynamic: this was shown in the ericoid belt of the Bale mountains of Ethiopia, where the
312 paleorecord evidenced a positive feedback between *Erica* abundance and fire (Gil-Romera
313 et al. 2019). A study from southwest Madagascar suggested similar, spatially heterogeneous
314 dynamics between littoral forest and *Erica/Myrica* grassland (Virah-Sawmy et al. 2009a).
315 Today, fire regimes in the central highlands are almost exclusively determined by humans;
316 fire is used, among other purposes, to control encroachment of *Erica* and other shrubs into
317 grassland (Kull and Lehmann 2022).

318

319 We currently do not know to what degree Malagasy *Erica* species differ in fire adaptations.
320 The high-altitude species of the ericoid thicket also appear to be very flammable, but it is
321 unclear whether this represents an adaptation or a vulnerability. At least some of the high-
322 altitude species resprout quickly after fire (Perrier de la Bâthie 1927a). Natural, lightning-lit
323 fires probably occur in the ericoid thicket (Crowley 2004, Gautier et al. 2018) – a possibility
324 ruled out by Perrier (1927a) – but at much lower frequencies than in the highlands or coastal
325 areas. Perrier himself acknowledged the role of *Erica* as pioneer shrubs, quickly resprouting

326 or colonising after fire and acting as nurseries for other plants (Perrier de la Bâthie 1927b).
327 *Erica* species of the high mountains of East Africa were similarly found to be adapted to low-
328 frequency fires (Fetene et al. 2006, Hemp 2006, Wesche 2006, Gil-Romera et al. 2019).
329 Both ‘resprouter’ and ‘seeder’ fire strategies seem to occur among the Malagasy *Erica* (M.P.,
330 pers. obs.); observations from Cape *Erica* species (Ojeda 1998) suggest that the higher-
331 altitude, more humid conditions would favour seeders, while the more pronounced drought
332 season at lower elevation would select for resprouters. Surveys of *Erica* root systems could
333 show whether there are species with lignotubers (Verdaguer and Ojeda 2002), and the
334 impact of fire on seed germination could be compared among species. Growth form, leaf
335 shape and leaf disposition probably also impact properties as fuel bed (Keeley et al. 2011,
336 Grootemaat et al. 2017) and should be examined for Malagasy *Erica*. This would help
337 understand e.g. to what degree escaping agricultural fires from lower altitudes harm the
338 ericoid thicket, and the conditions under which *Erica* stands fuel fires that can damage
339 adjacent remnants of forest.

340

341 There has been little further research on the ecology of Malagasy *Erica*. Most species are
342 found on the volcanic and metamorphic substrate of the high mountains and the lateritic soils
343 of the central highlands. Some appear to be specific to quartzite plateaus or the
344 southwestern Isalo sandstone range, and a single species, *Erica barnettiana* Dorr &
345 E.G.H.Oliv., was described from calcareous substrate, specifically cipollino marble west of
346 Ambositra (Perrier de la Bâthie 1927b). An endemic genus of springtails, *Anjavidrella*, is
347 confined to litter under *Erica* on the high mountains; four species have been described from
348 Ankaratra and Andringitra, but it has been suggested the genus may have radiated “as
349 explosively as *Erica*” on the island (Betsch 2003). Ericoid mycorrhiza has not been studied in
350 *Erica* or other Ericaceae in Madagascar. We also have not found any study of pollination in
351 Malagasy *Erica*, but one of us (M.P.) has observed mitrastylous species flowering in the
352 field: In contrast to those with a discoid stigma, they did not appear to release pollen into the
353 air on disturbance, suggesting insect rather than wind pollination. Potential pollinators of

354 these species remain to be identified. No seed information is available for Malagasy *Erica*;
355 Perrier (1927b) suggested the seeds disperse easily and retain their viability for long periods
356 in the soil. He also hypothesised that migratory birds may have carried *Erica* seeds between
357 Africa, Madagascar and the Mascarenes and specifically cited overlap in the ranges of the
358 common quail, *Coturnix coturnix*, and *Erica* in the central highlands of Madagascar (Perrier
359 de la Bâthie 1927b).

360

361 Ericaceae pollen has been recorded in Madagascar since the late Pleistocene (Fig. 4). We
362 found 17 palynological studies of sediment chronosequences, mostly from lakes, of which 10
363 recorded Ericaceae pollen (Table S2). Only one study identified *Erica* pollen to genus (Virah-
364 Sawmy et al. 2009b). The oldest sequence containing Ericaceae extended to c. 63 kyr cal
365 BP (Totorofotsy wetland in the eastern part of Madagascar; Straka 1996). Three
366 sequences from the central highlands extending into the last glacial period of the Pleistocene
367 (>11.7 kyr cal BP), all three from the central highlands, recorded high to dominant levels of
368 Ericaceae; this was interpreted as ericoid thicket spreading into lower-elevation zones during
369 cooler and drier periods (Gasse and Van Campo 1998, Straka 2001). High levels of
370 Ericaceae were also recorded in the gradually warming early Holocene in the central
371 highlands, and levels then decreased toward the present (Burney 1987b, 1987a, Straka
372 1996, Razafimanantsoa 2022). Burney (1987b) noted that central highland pollen was
373 “probably most likely *Philippia*, by far the most common ericoid genus in Madagascar”. By
374 contrast, in modern *Erica* grassland on the southeastern coast, Virah-Sawmy (2009b,
375 2009a) found an increase of Ericaceae and associated taxa toward the present, especially
376 around 950 BP, interpreted as a shift from forest and woodland to *Erica* grassland. Finally,
377 sequences from the eastern Alaotra wetland system, eastern littoral forest fragments, and
378 from the north and northwest, recorded only low levels of 10% or less throughout the
379 sequences (Matsumoto and Burney 1994, Straka 1996, Virah-Sawmy et al. 2009b,
380 Reinhardt et al. 2022, Broothaerts et al. 2023).

381

382 The overall picture of a high-mountain ericoid thicket being widespread in highland
 383 Madagascar during the last glacial period and then receding to the high mountains appears
 384 consistent with reconstructed paleoclimate (Gasse and Van Campo 1998). However, the
 385 present distribution of *Erica*, and other Ericaceae, extends far beyond the ericoid thickets
 386 biome (Fig. 3). There are also only a few published pollen spectra from modern vegetation in
 387 Madagascar that can be used as references for the interpretation of ancient pollen counts
 388 (Burney 1988, Straka 1991, Razafimanantsoa and Razanatsoa 2024). *Erica* can form dense
 389 thickets in the present-day central highlands (see Ecology section), which could also yield
 390 high local pollen counts. The studies of Virah-Sawmy et al. (2009b, 2009a), set near the
 391 south-eastern coast, also show that high levels of *Erica* may reflect an environment quite
 392 different from the montane thickets. The lack of resources for species identification,
 393 knowledge of the ecology of *Erica* and other Ericaceae, and clearly identified pollen
 394 reference material, also severely limit the interpretation of the palaeo-record. Ericaceae
 395 pollen, including from *Erica*, occurs mostly in tetrads, and the exine is characterised by the
 396 presence of numerous minute granules as secondary sculpture (Sarwar and Takahashi
 397 2014). Straka (1991) noted for Madagascar that “it is impossible to distinguish *Philippia*
 398 [pollen] tetrads”, based on light microscopy. However, a recent scanning-electron
 399 microscope study of *Erica* pollen found differences in pollen aggregation, size, shape and
 400 exine ornamentation between species (Wrońska-Pilarek et al. 2018). Four Malagasy taxa
 401 included in this study all had pollen in tetrads, but differed in other aspects of pollen
 402 morphology. This suggests that the collection and characterisation of pollen reference
 403 material for the extant Malagasy *Erica* species may yield features diagnostic for species or at
 404 least species groups, which combined with better knowledge on the ecology, may improve
 405 the resolution of the palaeo-record.

406
 407 **Uses and conservation**

408
 409 Only a few traditional uses have been documented for Malagasy *Erica* species. They are
 410 used mainly by Merina and Betsileo people from the central highlands, but also by

411 Betsimisaraka people from the eastern region. The genus *Erica* is clearly delimited from
 412 *Agarista* and *Vaccinium* by a folk taxonomy based on local ecological knowledge in dialects
 413 of the Malagasy language. For *Agarista* and *Vaccinium* respectively, 15 and 17 local names
 414 have been reported, mostly corresponding to clearly identified species (Schatz 2005), but for
 415 *Erica* only five: *anjavidilahy*, *anjavidy*, *riadriatra*, *kisiasia* and *anjavidilahimadinika* – the most
 416 commonly used being *anjavidy*, an ethnospecies encompassing several taxonomic species.
 417 The term *anjavidy* is formed from *anjaka*, “the action of tying into bundles” and *vidy*: “price,
 418 value“, which refers directly to its main use as firewood (de Veyrières and de Méritens 1967,
 419 Boiteau et al. 1980). In the past, trade in heather as firewood was particularly important and
 420 offered high returns (Boiteau et al. 1980). This wood was mainly used by affluent families
 421 and was highly appreciated for its fragrance when burned. The term *riadriatra*, mainly used
 422 by Betsileo, also refers to this use, the term being built on *riatra*: “which makes noise when
 423 set on fire”. By extension, *anjavidy* can also refer to species other than *Erica* that share
 424 similar characteristics (mainly flammability), such as *Hibbertia coriacea* Baill. (Dilleniaceae)
 425 and *Myrothamnus moschatus* (Baill.) Baill. ex Nied. (Myrothamnaceae) (Boiteau et al. 1980).

426 While the most widespread use of *Erica* in Madagascar is for fuel (Gade and Perkins-
 427 Belgram 1986), species of the genus probably have several other uses, for the time being
 428 not all documented. *Erica* branches are used as brooms (*kifafa-anjavidy*, “heather brooms”;
 429 Fig. 5e-f), but also as thatch for the roofs of Betsileo houses and as the preferred support for
 430 silkworm cocoons in traditional nurseries (Perrier de la Bâthie 1927b, Vernier 1964). In
 431 addition, some studies mention the use of *Erica* in traditional medicine: as cough treatment
 432 (Kull 2002), an anti-fever decoction from leafy branches (Onjalalaina et al. 2021) or for
 433 treating wounds, according to Betsileo traditional practitioners (V.P., unpublished). Finally,
 434 heathers are used by farmers as indicator plants for exhausted soils. After the passage of
 435 fire on an agricultural or forest plot, heather forms a dense secondary vegetation known as
 436 *savok'anjavidy* (literally, “heather fallow”). Farmers avoid these areas for cultivation (Carrière
 437 et al. 2005).

438 The conservation status of Malagasy *Erica* has not been formally assessed under the
439 International Union for the Conservation of Nature (IUCN) red list criteria. However, at least
440 one-fifth of the Malagasy species are likely to be threatened, according to a machine
441 learning prediction for the whole of Madagascar's flora, based on recorded occurrences and
442 environmental predictors (Ralimanana et al. 2022); Fig 6a). Seven out of 34 assessed *Erica*
443 species (20.5%) had a combined likelihood >0.5 to be threatened (critically endangered,
444 endangered or vulnerable; Fig. 6a); of these, five had a likelihood >0.5 to be critically
445 endangered: *Erica armandiana* Dorr & E.G.H.Oliv., *E. cryptoclada*, *E. goudotiana*, *E.*
446 *quadratiflora* and *E. wangfatiana* Dorr & E.G.H.Oliv. Surprisingly, this includes two rather
447 widespread species (*E. cryptoclada* and *E. goudotiana*). "Agriculture" was predicted as likely
448 threat category for 29 of the Malagasy *Erica* species, which is in line with the results of
449 Ralimanana et al. (2022) for the whole of the Malagasy flora, where Agriculture and
450 overexploitation affected 90% of all plant species. The central highlands, corresponding to
451 much of the *Erica* range, are the most densely populated area of Madagascar and used for
452 field cultivation and cattle farming. "Energy/mining" was predicted as a threat for 27 species
453 and appears likely, given the widespread use of *Erica* as firewood; a better understanding of
454 the species collected will be important. Mining could in particular affect the southern littoral
455 habitats which have partly been cleared for mining purposes (Virah-Sawmy 2009). "System
456 modification" was predicted for 21 species; this could correspond to changing fire regimes.
457 Fire was cited as the most important threat for the high-altitude ericoid thicket (Crowley
458 2004), but many *Erica* species also seem to require a minimum fire regime (see Ecology
459 section above). "Overexploitation" overlaps with use for "Energy" in the case of *Erica* and
460 was only predicted for five species, and "Pollution" only for one species. More basic research
461 on individual *Erica* species is needed to identify threats and enable formal conservation
462 assessments.

463
464
465

Conclusion and research priorities

466 (1) *Taxonomic revision*. The synthesis of taxonomy and diagnostic traits that we have now
467 incorporated into WFO and the *Erica* Identification Aid should help to some extent in
468 identifying *Erica* species in Madagascar. Particularly for non-specialists, the combination of
469 Latin and French descriptions presented in Perrier (1927a) may not have been
470 straightforward to interpret. However, this is unlikely to have been the main stumbling block
471 leading to the high proportions of undetermined collections apparent today. Perrier's work
472 was based on material available around 100 years ago, and his approach in defining
473 relatively narrow species concepts whilst describing numerous exceptions might reflect real,
474 complex variation but does not necessarily help in putting names to specimens. A modern
475 revision integrating molecular data to test species boundaries is sorely needed.

476

477 (2) *Phylogenomics*. Phylogenetic marker sets employed so far are clearly not sufficient to
478 resolve relationships within the Malagasy clade. More markers with greater numbers of
479 variable characters, e.g. using targeted sequence capture (Musker et al. 2024), will be
480 needed both to improve resolution and to test hypotheses of hybridisation, biogeography
481 and trait evolution in this rapid radiation. Uncertainty remains as to the positions of 22
482 Malagasy species which are either yet to be sequenced or cannot yet be unambiguously
483 attributed to undetermined collections (Appendix 1).

484

485 (3) *Ecology*. Very little ecological information can currently be attributed to species, and
486 Malagasy *Erica* are commonly treated as a single functional group. Yet the broad distribution
487 in Madagascar and the radiation into at least 35 species suggest significant variation. The
488 existence of both wind- and insect-pollinated species should be verified in the field. Better
489 understanding variation in fire and disturbance ecology between species would directly
490 inform land management and conservation. Improving resolution and functional
491 interpretation of the pollen record would contribute to a better understanding of the central
492 highlands' debated vegetation history. It will be essential to tie field studies and the collection

493 of trait data to herbarium voucher specimens, so that observed variation can be traced
494 through an evolving taxonomy.

495

496 (4) *Conservation*. The lack of taxonomic revision and resources currently hinder formal
497 conservation assessments. The preliminary estimate that at least one-fifth of the Malagasy
498 *Erica* species are threatened appears conservative in light of the threats facing
499 Madagascar's biota in general (Ralimanana et al. 2022). Missing taxonomic and ecological
500 information also prevents effective in situ and ex situ conservation. While species of the
501 high-altitude thickets may mostly be covered by existing protected areas, the status of
502 central highland and coastal species is unclear. Only two ex situ collections of Malagasy
503 *Erica* exist in the Millenium Seed Bank as of November 2024, both with unclear species
504 identities. Finally, recording traditional uses, which likely include more than the ones we
505 reported, will both aid in devising effective conservation strategies and help preserve
506 traditional knowledge.

507

Appendix 1

508

509 The 35 species of *Erica* L. currently accepted in Madagascar (Antonelli et al. 2022, Elliott et al. 2024, World Flora Online 2024), with World

510 Flora Online (WFO) and Global Biodiversity Information Facility (GBIF) identifiers and notes on distribution and ecology (unless otherwise

511 specified, following Perrier¹) and diagnostic traits (mostly summarised from Perrier¹), and Perrier's¹ numbering system (#) with subsequently512 described species incorporated according to documented similarity. Sources: ¹Perrier (1927), ²Dorr & Oliver (1999), ³GBIF occurrence data513 (<https://doi.org/10.15468/dl.pmcvqr>) – see also species occurrence maps in Fig. S1.

514

515

Species	Distribution	DN A dat a	Diagnostic descriptions	Notes	#
<i>Erica andringitrensis</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000671368 https://www.gbif.org/species/5683023	Andringitra ¹	N	Branched shrub, 1-2 m; leaves in whorls of 4; flowers solitary, arranged in leafy spike-like inflorescences along branches; stamens free, discoid stigma with inconspicuous lobes.		9
<i>Erica armandiana</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000671417 https://www.gbif.org/species/5682917	Central highlands ²	N	Plants more or less glandular, leaves in whorls of 4; flowers in terminal clusters; pedicel 2 mm long, surrounded by slightly differentiated leaves; large, bristly, glandular sepal without a dorsal slit; filaments fused only at the base; stigma lobes not extending beyond disc.	Similar to <i>E. hebeclada</i> and may fall within the variation in that species.	18
<i>Erica barnettiana</i> Dorr & E.G.H.Oliv.	Central highlands	N	Narrowly branched shrub with white-pubescent branches; leaves opposite, superimposed in 4 rows completely hiding the	The only Malagasy species growing on	8

https://list.worldfloraonline.org/wfo-0000671480 https://www.gbif.org/species/5682775	(Ivato basin west of Ambositra) ¹		stem; stamens connate; stigma lobes not extending beyond disc.	limestone. ¹	
<i>Erica baroniana</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000671481 https://www.gbif.org/species/5682773	Central highlands and eastern coast ¹	N	Erect shrub (" <i>Erica scoparia</i> -like habit") with spindly greyish pubescent branches; leaves in whorls of 3 (2 on young branches), 2-4 mm long, spreading or ascending but not adnate to stem; flowers in terminal clusters of 3-7, not subtended by differentiated leaves; corolla 1.3 mm long, valvate; stigma lobes not extending beyond disc.	Common, widespread and very variable.	34
<i>Erica betsileana</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000671503 https://www.gbif.org/species/5682711	Central highlands: quartzite mountains between Ivato and Mania basins ¹	N	Lax, green shrub; leaves distant, spreading/recurved; short glandular bristles; 8 stamens adnate at base; 4 long stigmatic lobes and reflexed tubular disc.	Similar to <i>E. parkeri</i> and <i>E. humbertii</i> , differing in habit (shrubby in <i>E. parkeri</i>) and indument (long non-glandular bristles in <i>E. humbertii</i>)	5
<i>Erica bojeri</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000671524 https://www.gbif.org/species/5682663	Central highlands (Imerina) ²	Y	Stem hairy, brownish; internodes longer than the leaves; leaves in whorls of 4; petiole 0.25 mm, blade 1.5-2 mm long, dorsal and ventral surfaces domed, with a very narrow dorsal slit, covered with small, fairly sparse brownish hairs, with a long-stalked (up to 2/3 as long as the leaf) gland at the apex; flowers in terminal clusters (3-5), pedicel 2 to 3 mm long, not surrounded by differentiated leaves; calyx with obtuse, pubescent lobes bearing a few glands, the largest without a dorsal slit, reaching the middle of the corolla; 7-8 stamens with filaments free to the base; style strongly bristly towards the (swollen) base, stigma lobes not extending beyond disc.	Similar to <i>E. hebeclada</i> , maybe just a variant. ¹	21

<p><i>Erica bosseri</i> Dorr https://list.worldfloraonline.org/wfo-0000671534 https://www.gbif.org/species/5682642</p>	Ankaratra ²	N	Low, erect or decumbent shrub 0.3 m tall with reddish pubescent branches; leaves with glandular and simple hairs, terminating in a very stout, 0.8-1 mm long, gland-tipped hair that forms an acute angle with the plane of the leaf blade; calyx lobes broadly obovate or narrowly oblanceolate to oblanceolate with glandular pubescence; narrow corolla mouth, anthers included within the corolla, style hairy with 4 long stigmatic lobes and reflexed tubular disc.	Similar to <i>E. madagascariensis</i> from which it differs chiefly in the hairs of the leaves, in the shape and size of the sepals, and especially in the shape of the corolla. ²	1(b)
<p><i>Erica boutonii</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000671540 https://www.gbif.org/species/5682634</p>	Central highlands (Imerina) ¹	Y	Shrub with white-pubescent branches but without glandular hairs, leaves in whorls of 4, overlapping and hiding the stem; flowers in terminal clusters surrounded by slightly differentiated leaves, stigma discoid with slightly projecting lobes.	Similar to <i>E. leuoclada</i> which has stamens fused on lower half only and broader stigmas. The var. <i>cinerea</i> ¹ has greyish appearance due to denser indument.	11
<p><i>Erica cryptoclada</i> (Baker) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000671793 https://www.gbif.org/species/5682053</p>	Central highlands, (Tsarantanan a and Marojejy to Isalo) ¹ – records also from Andohahela ³	Y	Shrub with white pubescent branches; leaves in whorls of 3, < 6 mm long, very appressed on the stem, closely imbricate, with sessile black corpuscles on the margins; flowers in terminal clusters of 3-7, not subtended by differentiated leaves, corolla <2 mm long with overlapping lobes with toothed margins, stigma lobes visible.	Widespread and variable; “var. <i>hybrida</i> ” H.Perrier (considered synonymous ²) found under tapia in Isalo.	30
<p><i>Erica danguyana</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000671793</p>	Central highlands (Antsirabe) ¹	N	Shrub of 1 to 2 m., hairy but without glands, leaves ≥4x as long as wide, in whorls of 4, not hiding stem; flowers in terminal clusters, 8 connate stamens, discoid stigma with	Similar to <i>E. boutonii</i> but differing in longer	10

org/wfo-0000671839 https://www.gbif.org/species/5681963			inconspicuous lobes.	leaves and pedicels and in the larger, thick sepals that extend beyond the corolla	
<i>Erica densata</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000671864 https://www.gbif.org/species/5681923	Disjunct populations at Manongarivo and Tsaratanana in the north; central highlandst ¹	N	Shrub with tomentose branches; hairs non-glandular, branched; leaves in whorls of 3 or 4, internodes c. 1mm (shorter than diameter of stem), overlapping and hiding the stem; flowers in terminal clusters surrounded by slightly differentiated leaves, stigma lobes not extending beyond disc.	Differs from <i>E. boutonii</i> by the much thicker, larger calyx with keeled sepals, at least the largest of which has a dorsal slit. Distinct local forms (specimens from the north reaching 3-4 m) ¹ .	16
<i>Erica goudotiana</i> (Klotzsch) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672181 https://www.gbif.org/species/8632971	Tsaratanana, Central Highlands, Itremo, East coast ¹	N	Shrub 1-2 m tall (but see wider variation), branches with white indument, leaves in whorls of 3, largely glabrous, without spines at apices; flowers solitary, subtended by 3-4 narrow, yellowish leaves, largest sepal as long as petals, the rest reaching bases of petal lobes, all glabrous but ciliate at margins; stigma lobes inconspicuous.	Perrier's description matches the common form only: he described subspecific taxa (such as ' <i>Philippia cauliflora gigas</i> ', reaching 5-6 m in height) and reported 'innumerable' deviating forms. ¹ Species complex.	24
<i>Erica hebeclada</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672181	Central highlands, Ankaratra,	Y	Shrub with upright habit; stem whitish pubescent; abundance of glands on the stems, leaves, pedicels and calyces; leaves in whorls of 4 often ascending and elongated; petioles 0.6-1 mm	Variable: two varieties differing in e.g. leaf shape and	19

org/wfo-0000672221 https://www.gbif.org/species/5684867	Andringitra ¹ – records also from Isalo ³		long, blade 2 to 3 mm, domed above, with a clear dorsal slit; flowers in terminal clusters (3-6), pedicel 1.5 mm long, not surrounded by differentiated leaves; calyx bristly, glandular, largest sepal without a dorsal slit, not reaching the corolla sinuses; filaments entirely fused; style bristly at base, stigma lobes not extending beyond disc but clearly visible in profile on the fresh flower.	distribution of indument ¹ .	
<i>Erica humbertii</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672270 https://www.gbif.org/species/5684738	Andringitra ¹	Y	Low sprawling green plant, leaves distant, spreading/recurved, very long non-glandular bristles on stems and leaf tips, 3-4(-6) stamens, 4 long stigmatic lobes and reflexed tubular 'disk.		3
<i>Erica ibityensis</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672285 https://www.gbif.org/species/5684706	Central highlands (Ibity) ¹	N	Shrub up to 1.2 m, stiff grey pubescent branches, without glandular hairs, leaves in whorls of 4, overlapping and hiding the stem; flowers in terminal clusters surrounded by wider, thinner, sessile leaves, stigma lobes inconspicuous.		14
<i>Erica imerinensis</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672293 https://www.gbif.org/species/5684685	Central highlands: south of Tsinjoarivo ¹	N	Rigid shrubs with white pubescent branches; leaves in whorls of 3, <6 mm long, narrowly imbricate, loosely erect against the stem and hiding it, glabrous but with very short, stalked glands when young; flowers in terminal clusters of 3-7, not subtended by differentiated leaves, corolla <2 mm long with overlapping lobes, stigma lobes inconspicuous.		29
<i>Erica isaloensis</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672347 https://www.gbif.org/species/5684596	Isalo ¹	Y	Dwarf plant; leaves in whorls of 4, upright hiding the stem, with domed upper surfaces and narrow slit; corolla glabrous, 8 free stamens, stigma with prominent lobes extending beyond disc.		7

<p><i>Erica jumellei</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672364 https://www.gbif.org/species/5684573</p>	<p>Central highlands (Arivonimamo)¹</p>	<p>N</p>	<p>Shrub with slender branches (1.5-2.5 mm diam.), without glandular hairs, leaves in whorls of 3 (2, 4), overlapping and hiding the stem; flowers in terminal clusters surrounded by slightly differentiated leaves, stigma discoid with inconspicuous lobes.</p>	<p>Similar to <i>E. densata</i> and <i>E. boutonii</i> but leaves and flowers are smaller; sepals shorter and not split at the back (cf. <i>E. densata</i>); and with a large carinate sepal (cf. <i>E. boutonii</i>)¹.</p>	<p>12</p>
<p><i>Erica lecomtei</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672443 https://www.gbif.org/species/7328672</p>	<p>- subsp. <i>lecomtei</i>: central highlands (Ibity, Itremo)² - subsp. <i>ravinakely</i> Dorr: Isalo²</p>	<p>N</p>	<p>Shrub 1 to 4 m tall; leaves in whorls of 3, 8-10 mm long, erect hiding the stem, narrow-lanceolate-linear with scaly, denticulate margins, dorsal slit narrow, leaving neither the midrib nor the underside of the leaf blade visible; flowers in terminal clusters of 3-5, not subtended by differentiated leaves; corolla 5 mm long with 2 mm lobes, stigma lobes not extending beyond disc.</p>	<p>Similar to <i>E. viguieri</i>.</p>	<p>28</p>
<p><i>Erica leucoclada</i> (Baker) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672464 https://www.gbif.org/species/5684343</p>	<p>Central highlands (North Antsihanaka) – records also from Mandena (east coast)³</p>	<p>N</p>	<p>Shrub with white-pubescent branches but without glandular hairs, leaves in whorls of 4 (3,2), overlapping and hiding the stem; flowers in terminal clusters surrounded by slightly differentiated leaves, filaments fused along lower half, stigma discoid, broad (1.25 mm), with slightly protruding lobes.</p>		<p>13</p>
<p><i>Erica lyallii</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672520</p>	<p>Central highlands (Ankaratra, Ibity)¹ –</p>	<p>N</p>	<p>See <i>E. baroniana</i>.</p>	<p>Considered doubtful¹; perhaps a form of <i>E. baroniana</i> or</p>	<p>34(b)</p>

https://www.gbif.org/species/5684247	records also from Kalambatritra (south) ³			similar. <i>Philippia floribunda glandulosa</i> H. Perrier synonymous ² .	
<i>Erica macrocalyx</i> (Baker) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672539 https://www.gbif.org/species/5684207	Central highlands ¹	N	Shrub with bristly branches without glandular hairs, leaves in whorls of 4, overlapping and hiding the stem; flowers in terminal clusters surrounded by slightly differentiated leaves, filaments fused, stigma not exerted, discoid, 1 mm diam., with raised margins hiding the lobes.		15
<i>Erica madagascariensis</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672547 https://www.gbif.org/species/5684195	Central highlands, Ankaratra ²	Y	Low growing, very hairy greyish shrub, erect leaves hiding stems; sepals narrow, long ciliate; style hairy with 4 long stigmatic lobes and reflexed tubular disc.	Similar to <i>E. bosseri</i> .	1/2
<i>Erica marojejyensis</i> Dorr https://list.worldfloraonline.org/wfo-0000672576 https://www.gbif.org/species/5684138	Marojejy ²	N	Distinguished from <i>E. lecomtei</i> by its spreading (versus imbricate and rigidly ascending) leaves that are pubescent (versus glabrous) adaxially and by its calyx in which the longest calyx lobe slightly exceeds the corolla in length. The longest calyx lobe in <i>E. lecomtei</i> is shorter than the corolla in length. Distinguished from <i>E. viguieri</i> by its shorter (2.5-5.2 versus 6.5-12 mm long) and narrower (1.5-2 versus 2-2.8 mm wide) leaves that have a closed (versus open) sulcus. Additionally, the inflorescences of <i>E. marojejyensis</i> have many fewer (3 versus 9) flowers than those of <i>E. viguieri</i> .	Similar to <i>E. lecomtei</i> and <i>E. viguieri</i> ² .	28(b))
<i>Erica minutifolia</i> (Baker) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672623	Central highlands ²	N	Stems greyish pubescent with short stalked glands; leaves usually 4; petiole 0.25-0.5 mm; blade 1-1.5, with small protuberances on the margins; flowers in terminal clusters, pedicel 1.5-3 mm long, bristly glandular, not surrounded by	Similar to <i>E. bojeri</i> ; includes Perrier's concept of <i>E. oophylla</i> which	22/2 3

https://www.gbif.org/species/5684041			differentiated leaves, the large sepal without a dorsal slit slightly exceeding the middle of the corolla; 8 stamens with filaments united at the base; style long (2.5 mm) with a few bristles towards the base, stigma lobes not extending beyond disc.	represents variation with larger leaves and longer pedicels.	
<i>Erica myriadenia</i> (Baker) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672681 https://www.gbif.org/species/5683931	Central highlands ¹	Y	Plants more or less glandular, leaves in whorls of 4, flowers in terminal clusters, sessile, surrounded by slightly differentiated leaves, with large, bristly, glandular sepal without a dorsal slit, filaments entirely fused, stigma lobes not extending beyond disc.	Widespread and variable ¹ .	17
<i>Erica parkeri</i> (Baker) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672822 https://www.gbif.org/species/5683749	Central highlands ¹	Y	Shrubby green plant, leaves distant, spreading/recurved, short glandular bristles, 8 adnate stamens, 4 long stigmatic lobes and reflexed tubular disc.	Very variable; differs from <i>E. humbertii</i> by its glandular bristles, and adnate (as opposed to free) stamens ¹ .	4
<i>Erica perhispida</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672870 https://www.gbif.org/species/5683659	Central highlands, Tsaratanana ¹	N	Spindly, recumbent plant, all parts with glandular hairs; leaves in whorls of 4, petiole 0.5-0.75 mm, blade variable, 1-2 mm, oval or ovate-lanceolate on the same branch, backs somewhat open; flowers in terminal clusters (3-5), not surrounded by differentiated leaves,; 1-1.5 mm long, largest sepal without a dorsal slit; 8 stamens fused partly or almost to the apex, style bristly at base, stigma lobes prominent, extending beyond disc (or not).	Status of local variant " <i>Philippia hispida angustifolia</i> " H. Perrier from Tsaratanana unclear. ² <i>Philippia adenophylla</i> Baker (#20) considered synonymous ²	6/20
<i>Erica perrieri</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672877	Andringitra, Ibity ¹	Y	Branched shrub 1-4 m tall, leaves in whorls of 3, ovate, open-backed, >6 mm long, glabrous; flowers in terminal clusters of 3-7, not subtended by differentiated leaves; stigma lobes visible.		26

https://www.gbif.org/species/5683647					
<i>Erica quadratiflora</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000673059 https://www.gbif.org/species/5683223	Andohahela ² – widely disjunct records also from the northern Sambava region ³			Published in Perrier (1930) - details pending	-
<i>Erica rakotozafyana</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000673076 https://www.gbif.org/species/5683190	Central highlands, Andringitra ¹ – records also from the southeastern coast ³	Y	Shrub up to 1 m tall, many slender branches with greyish indument; leaves in whorls of 3 (often 2 on young branches), < 6 mm long, narrowly imbricate, appressed, blackish; flowers in terminal clusters of 3-7, not subtended by differentiated leaves, corolla <2 mm long with overlapping lobes, stigma lobes not extending beyond disc.		31
<i>Erica spinifera</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000673295 https://www.gbif.org/species/5682712	Andringitra ¹	Y	Shrub 1-6 m tall, branches with grey indument; leaves in whorls of 3, serrated at margins, with 1.5 mm or longer 'spines' at apices (formed from adnate hairs; lost in older leaves); flowers solitary, subtended by 3-4 narrow, yellowish leaves, larger calyx lobe almost free, the others fused in lower third; stigma lobes inconspicuous.		25
<i>Erica sylvainiana</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000673362 https://www.gbif.org/species/5682545	Andringitra ¹	N	Low growing, cypress-like habit with rigid, slender, white-pubescent branches, other parts appearing glabrous; leaves in whorls of 3, 1-3 mm long, dimorphic: much smaller on flowering stems, spreading or ascending but not adnate to stem; flowers in terminal clusters of 3-7, not subtended by differentiated leaves, corolla 1.25 mm long, valvate, stigma lobes not extending beyond disc.		33

<p><i>Erica viguieri</i> (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000673574 https://www.gbif.org/species/5681980</p>	Andringitra ¹	N	Shrub 2-4 m tall, thick stem with very visible, closely spaced leaf scars; leaves in whorls of 3, 8-10 mm long, narrow-lanceolate-linear with scaly, denticulate margins, a dorsal slit revealing prominent midrib; flowers in large, nodding terminal clusters of 3-7, not subtended by differentiated leaves; corolla 4.5 mm long with 2 mm lobes, stigma lobes inconspicuous.	Similar to <i>E. lecomtei</i> .	27
<p><i>Erica wangfatiana</i> Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000673625 https://www.gbif.org/species/5681890</p>	Andringitra ¹	N	Rigid shrub with glabrous branches; leaves in whorls of 3, 2-6 mm long, half as short on small branches than on the others spreading or ascending but not adnate to stem; flowers in terminal clusters of 3-7, not subtended by differentiated leaves, corolla 1 mm long, valvate, subglobose; stigma lobes not extending beyond disc.	Similar to <i>E. baroniana</i> . ¹	32

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518

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526

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528

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530

531 **References**

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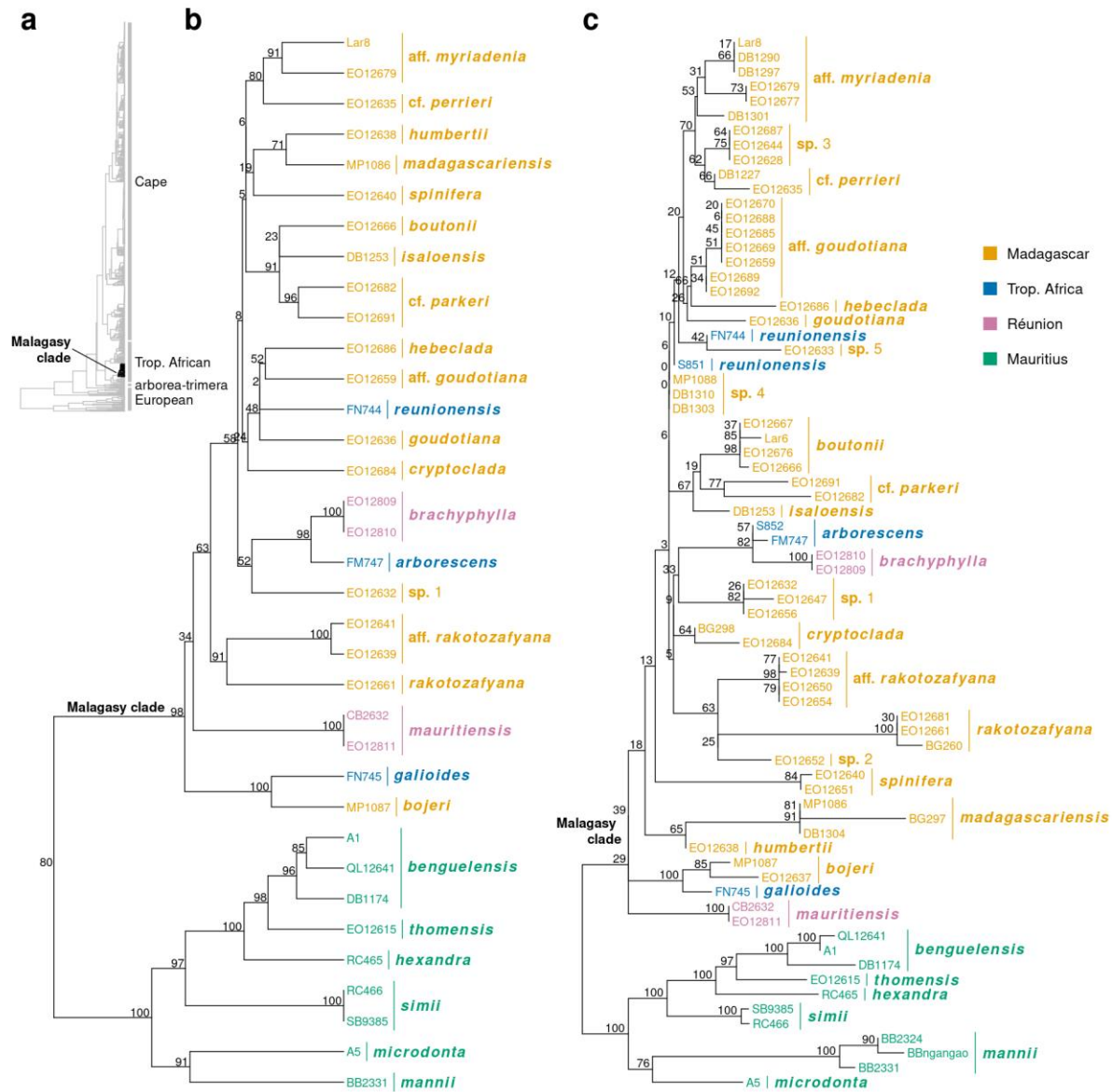
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808 **Figures**

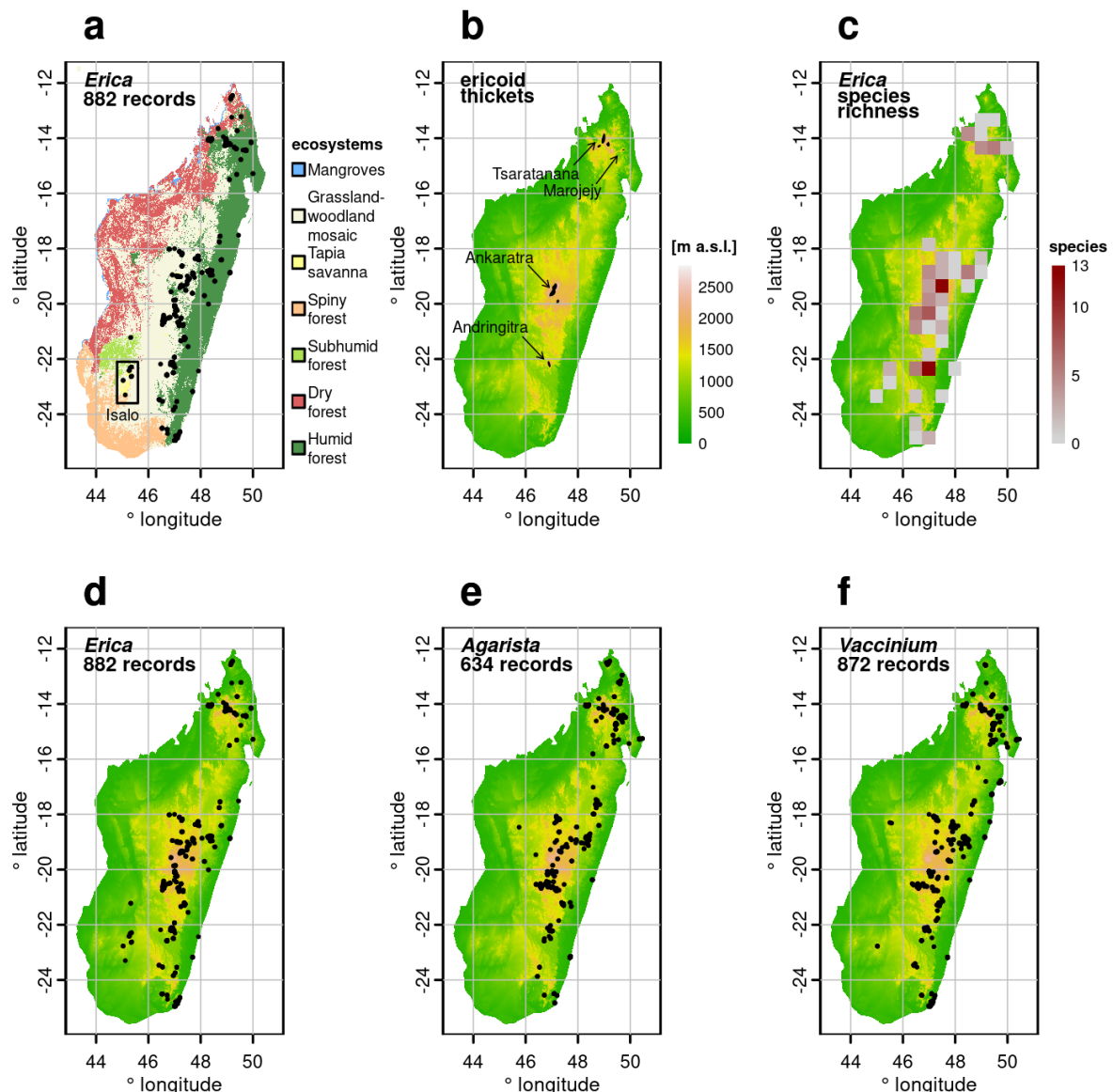


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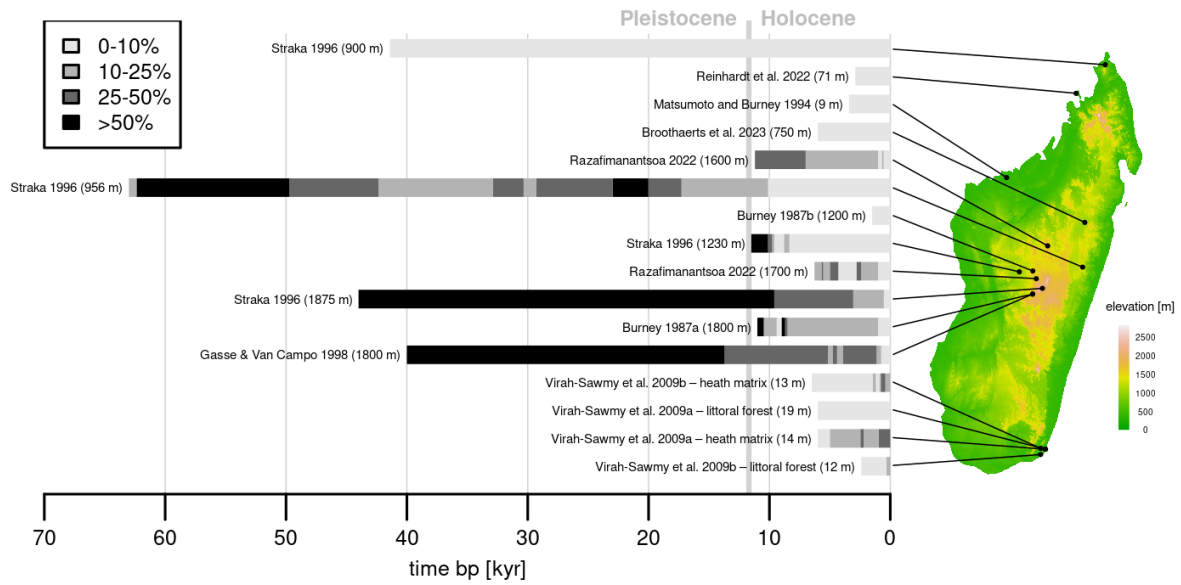
810 **Figure 1: Floral diversity of *Erica* in Madagascar.** A selection of specimens collected by
 811 E.G.H. Oliver and colleagues: A. *E. bojeri* (EO12649); B. *E. boutonii* Dorr & E.G.H.Oliv.
 812 (EO12676); C. *E. cryptoclada* (Baker) Dorr & E.G.H.Oliv. (EO12642); D. *E. hebeclada* Dorr
 813 & E.G.H.Oliv. (EO12690); E. *E. humbertii* (H.Perrier) Dorr & E.G.H.Oliv. (EO12648); F. *E.*
 814 *myriadenia* (Baker) Dorr & E.G.H.Oliv. (EO12677); G. *E. parkeri* (EO12626); H. *E. perrieri*
 815 (EO12635); I. *E. rakotozafyana* Dorr & E.G.H.Oliv. (EO12681). Photos: Michael D. Pirie.
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 819 **Figure 2: Phylogenetic relationships of Malagasy *Erica*.** (a) Position of the Malagasy
 820 clade in the genus according to (Pirie et al. 2024). The tree includes 771 accessions and
 821 several nuclear and plastid markers. (b) Focus on the Malagasy clade and its Tropical
 822 African sister clade (same tree as in a). (c) Tree estimated from the same marker set as in a-
 823 b but expanded with ITS for 36 additional accessions. Values on nodes are Felsenstein
 824 bootstrap support percentages.



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 826 **Figure 3: Distribution of *Erica* and other Ericaceae in Madagascar.** Occurrence data
 827 were obtained from the Global Biodiversity Information Facility and submitted to multiple
 828 filtering steps (see text). (a) *Erica* distribution plotted against the Madagascar ecosystem
 829 map of (Antonelli et al. 2022). See also records mapped per species in Fig. S1,
 830 supplementary material. (b) Distribution of the “Madagascar ericoid thickets” ecoregion
 831 (Dinerstein et al. 2017). (c) *Erica* species richness per 0.5x0.5 ° grid cell, summarised from
 832 occurrence records identified to species level. (d) Distribution of *Erica* in Madagascar
 833 compared to (e) *Agarista* and (f) *Vaccinium*, the other two genera of Ericaceae occurring in
 834 Madagascar.



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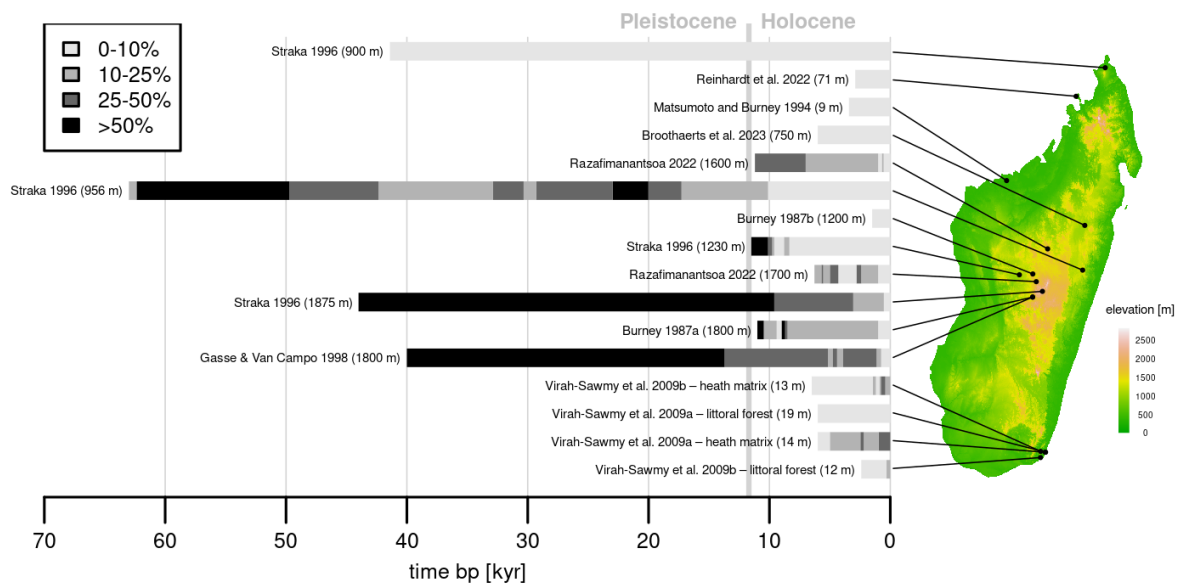
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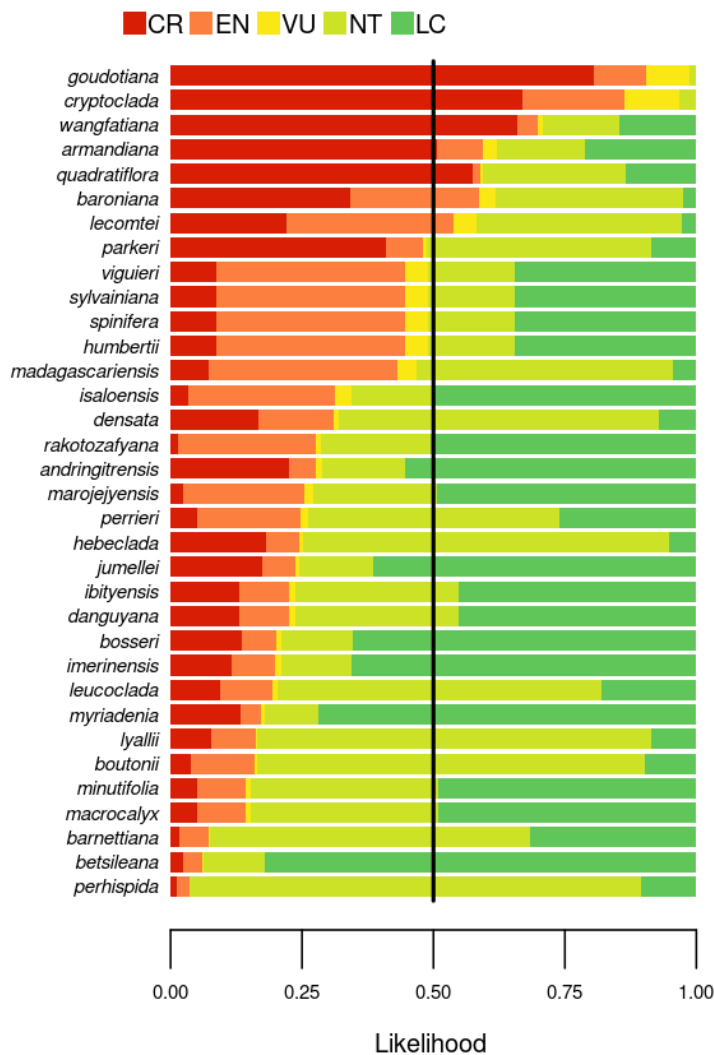
Figure 4: Habitats and uses of *Erica* in Madagascar. (a) *Erica* sp. in a mosaic with grassland, Andringitra National Park, Southeast, c. 2,000 m elevation. Lorna MacKinnon, Diana Rabeharison, Nantenaina Rakotomalala, and Fenitra Randrianarimanana 2022. (b) *Erica* sp. on coastal sand, Manombo Special Reserve, Southeast. Nina Lester Finley 2023 (CC BY 4.0), <https://www.inaturalist.org/observations/186728736>. (c) Tree heathers, probably corresponding to *Philippia cauliflora* subsp. *gigas* H.Perrier (now included in *Erica goudotiana* (Klotzsch) Dorr & E.G.H.Oliv), at campsite Beanjavidy (“the big heathers”), Tsaratanana Reserve, North, c. 2,300 m elevation. Andry Rakotoarisoa 2022. (d) *Erica* sp. colonising an opening dominated by the flammable grass *Aristida* cf. *rufescens* in Tsaratanana Reserve, at c. 2,000 m elevation. Jan Hackel 2022. (e-f) Cut bundles of two unidentified *Erica* species near Anfanifotsy, just outside Andringitra National Park, c. 1,500 m elevation. Vincent Porcher 2020 (CC BY), <https://www.inaturalist.org/observations/95638300>.



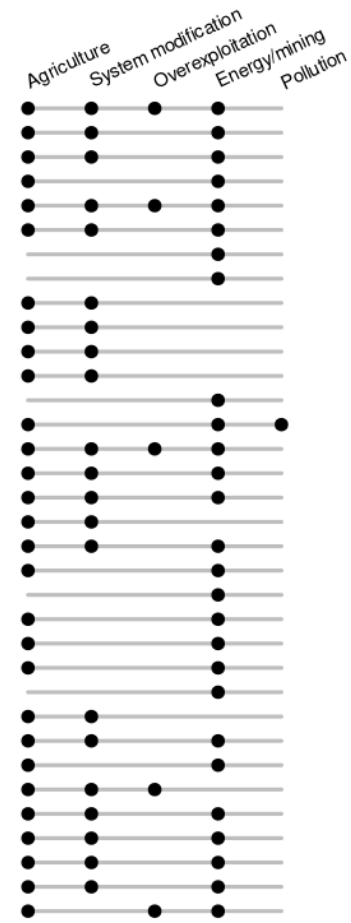
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Figure 5: Abundance of Ericaceae pollen over time as proportion of overall pollen counts in sediment chronosequences in Madagascar. Data shown were summarised manually from 11 studies that recorded Ericaceae (see table S2), varying in temporal extent and resolution. Only one study (Virah-Sawmy 2009b) identified *Erica* pollen to genus (*Vaccinium*, also identified, is not shown here). All other studies identified Ericaceae pollen only to family level. Data shown for Gasse & Van Campo (1998) are for “pollen group P1”, in which Ericaceae was the dominant taxon, and data for Virah-Sawmy (2009a) are for a pollen group grouping *Erica* with *Vaccinium*, *Asteraceae*, *Helichrysum* and graminoids. Data from Straka (1996) have only few calibration points and also include fern spores and aquatics in the total counts.

a Predicted conservation status



b Predicted threats



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861 **Figure 6:** Predicted conservation status and threats for Malagasy *Erica* species, from
 862 Ralimanana et al. (2022). International Union for the Conservation of Nature categories for
 863 (a) conservation status and (b) threats were predicted for all unassessed plant species of
 864 Madagascar using a neural network model based on species occurrences and associated
 865 environmental predictors, with existing plant assessments as training set (Zizka et al. 2022).
 866 CR: critically endangered, EN: endangered, VU: vulnerable, NT: near threatened, LC: least
 867 concern. *Erica bojeri* was not assessed.

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870 **Supplementary Material**

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872 **Figure S1.** Occurrences per identified Malagasy *Erica* species, plotted on elevation maps.

873

874 **Table S1.** Specimen information for new DNA sequence data. [Accession numbers will be
875 made available at publication]

876

877 **Table S2.** Information on *Erica* pollen abundance in sediment chronosequences extracted
878 from the literature.