Heathers (Erica, Ericaceae) of Madagascar: taxonomy, evolution, ecology and uses

Jan Hackel, Andriantsilavo H I Razafimanantsoa, Vincent Porcher, Michael D Pirie

PREPRINT

Author-formatted, not peer-reviewed document posted on 12/11/2024

DOI: https://doi.org/10.3897/arphapreprints.e141580

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

Jan Hackel, Andriantsilavo H. I. Razafimanantsoa, Vincent Porcher, Michael Pirie

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

Jan Hackel[1], Andriantsilavo H. I. Razafimanantsoa[2], Vincent Porcher[3], Michael D. Pirie[4]

[1]Philipps-Universität Marburg, Department of Biology, Marburg, Germany – ORCID: 0000-0002-9657-5372
[2]Human Evolution Research Institute, Department of Geological Sciences, University of Cape Town, South Africa – ORCID: 0000-0002-9933-6991
[3]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France – ORCID: 0000-0003-2879-6728
[4]University Museum, University of Bergen, Postboks 7800, NO-5020 Bergen, Norway – ORCID: 0000-0003-0403-4470

Abstract

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

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

Keywords

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

Introduction

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

Taxonomy

Of the currently recognised Ericaceae genera in Madagascar, *Erica* (Ericoideae; Ericeae) is easily distinguished from *Agarista* and *Vaccinium* (both Vaccinioideae), most obviously by its often needle- or scale-like leaves characterised by revolute margins almost touching on the underside (“ericoid leaves”), arranged in whorls of 3-6, and its persistent corolla enveloping the fruit (Oliver 2000, Schatz 2005). However, within *Erica* and the tribe Ericeae, generic bounds were a longstanding subject of debate that was only resolved towards the end of the last century.

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

Perrier (1927a) grouped the Malagasy species according to morphological characters which he ranked in order of importance. Most important was the shape of the stigma, on which Perrier defined two sections: I (Cornigerae) for species with expanded stigmatic lobes (including, but not limited to, the ‘mitrastylous’ species; his numbers 1-7, Appendix 1); and II (Discoidales) for those with a more typical discoid stigma (numbers 8-34). This was followed in descending order of importance by the arrangement of the leaves (particularly in whorls of three versus of four); indument (he distinguished four types differing e.g. by length and presence or not of glands); leaf shape; inflorescence structure (terminal clusters of flowers, or not); flower and style shape (particularly shape and relative size of sepals); and degree of fusion of the stamens. Some species are distinct and easily identified even from images, such as *E. perrieri* Dorr & E.G.H.Oliv. with its unique open-backed leaves (Fig. 1 H). Most of the others are less obvious.

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

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

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

Phylogenetics and evolution

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

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

ARPHA Preprints Author-formatted, not peer-reviewed document posted on 12/11/2024. DOI: https://doi.org/10.3897/arphapreprints.e141580

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

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

The additional ITS data added to the existing supermatrix of plastid and ITS/ETS data of Pirie et al. (2024) falls unambiguously within a monophyletic Malagasy/Mascarene clade, but does not result in a well supported internal topology. Undetermined collections that we tentatively grouped into morphospecies tended to show similar sequence variation (Fig. 2c), but such variation was low and the groupings unsupported. This is in contrast to within the *Erica* Cape clade, which represents an order of magnitude more species than the Malagasy clade but nevertheless shows enough variation in ITS to be able to test the relationships of individual specimens (Hoekstra et al., in prep.). The difference in sequence variation may be explained by a combination of younger age and/or faster diversification rates of Malagasy lineages. *Erica* is estimated to have arrived in Madagascar around 5-7 million years ago on the basis of relaxed clock molecular dating and a secondary Ericaceae calibration (Pirie et al. 2016). From these results, Pirie et al. (2016) estimated that the Malagasy clade may have one of the highest diversification rates in *Erica.* Given the dependence of these estimates on both absolute time calibration and relaxed clock assumptions, they should be revisited with further, phylogenomic data and ideally more calibration points. This would also allow reconstructing trait evolution within the Malagasy clade and testing e.g. for parallel evolution of insect pollination from a probably wind-pollinated ancestor.

Distribution and habitats

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

E baroniana Dorr & E.G.H.Oliv. These cases highlight persisting confusion in the taxonomy of Malagasy *Erica*.

Erica is found in all except the driest regions of Madagascar (Fig. 3). Plotting *Erica* occurrences against Madagascar’s ecosystems (Fig. 3a), following the map of Antonelli et al. (2022), shows that *Erica* is found in all major ecosystem types except the western dry forests and the southwestern spiny forest (and the coastal mangroves). This includes the grassland–woodland mosaic of the central highlands, humid forest, and tapia savanna. Two specimens only identified to genus suggest *Erica* may also occur in the Makay massif in southwestern Madagascar, at the northern edge of the “subhumid forests” area. The “ericoid thickets” (Crowley 2004), described in some vegetation classifications and defined by *Erica* and similar “ericoid” shrubs, are confined to the four highest mountain massifs: Tsaratanana, Marojejey, Ankaratra and Andringitra (Fig. 3b). According to other authors, vegetation of this type also occurs further south, on the summit of Andohahela (Goodman et al. 2018c). The ericoid thickets cover only c. 1,300 km^2 in total (Crowley 2004). The high mountains is also where the species richness of *Erica* is highest, peaking in the Ankaratra and Andringitra ranges, each with 13 species recorded per 0.5x0.5 ° grid cell (Fig. 3c). Six species appear to be endemic to Andringitra alone (Appendix 1). Perrier (1927b) named *Philippia floribunda* Benth. (= *Erica baroniana* Dorr & E.G.H. Oliv.) as the only species occurring at sea level in Madagascar, but *E. goudotiana* and *E. leucoclada* have also been recorded from the Eastern coast (Appendix 1, Fig. S1). The other two Ericaceae genera *Agarista* and *Vaccinium* have distribution patterns broadly similar to *Erica* in Madagascar (Fig. 3d-f); they have additionally been recorded from isolated humid forest areas of the western Bongolava region, which suggests *Erica* might also occur there.

Erica species in Madagascar are open-habitat shrubs or form their own canopy (Perrier de la Bâthie 1927b, Silander Jr. et al. 2024). Based on the literature, there appear to be three main habitat types:

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

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

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

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

Ecology and interactions

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

We currently do not know to what degree Malagasy *Erica* species differ in fire adaptations. The high-altitude species of the ericoid thicket also appear to be very flammable, but it is unclear whether this represents an adaptation or a vulnerability. At least some of the high-altitude species resprout quickly after fire (Perrier de la Bâthie 1927a). Natural, lightning-lit fires probably occur in the ericoid thicket (Crowley 2004, Gautier et al. 2018) – a possibility ruled out by Perrier (1927a) – but at much lower frequencies than in the highlands or coastal areas. Perrier himself acknowledged the role of *Erica* as pioneer shrubs, quickly resprouting or colonising after fire and acting as nurseries for other plants (Perrier de la Bâthie 1927b). *Erica* species of the high mountains of East Africa were similarly found to be adapted to low-frequency fires (Fetene et al. 2006, Hemp 2006, Wesche 2006, Gil-Romera et al. 2019). Both 'resprouter' and 'seeder' fire strategies seem to occur among the Malagasy *Erica* (M.P., pers. obs.); observations from Cape *Erica* species (Ojeda 1998) suggest that the higher-altitude, more humid conditions would favour seeders, while the more pronounced drought season at lower elevation would select for resprouters. Surveys of *Erica* root systems could show whether there are species with lignotubers (Verdaguer and Ojeda 2002), and the impact of fire on seed germination could be compared among species. Growth form, leaf shape and leaf disposition probably also impact properties as fuel bed (Keeley et al. 2011, Grootemaat et al. 2017) and should be examined for Malagasy *Erica*. This would help understand e.g. to what degree escaping agricultural fires from lower altitudes harm the ericoid thicket, and the conditions under which *Erica* stands fuel fires that can damage adjacent remnants of forest.

There has been little further research on the ecology of Malagasy *Erica*. Most species are found on the volcanic and metamorphic substrate of the high mountains and the lateritic soils of the central highlands. Some appear to be specific to quartzite plateaus or the southwestern Isalo sandstone range, and a single species, *Erica barnettiana* Dorr & E.G.H.Oliv., was described from calcareous substrate, specifically cipollino marble west of Ambositra (Perrier de la Bâthie 1927b). An endemic genus of springtails, *Anjavidiella*, is confined to litter under *Erica* on the high mountains; four species have been described from Ankaratra and Andringitra, but it has been suggested the genus may have radiated "as explosively as *Erica*" on the island (Betsch 2003). Ericoid mycorrhiza has not been studied in *Erica* or other Ericaceae in Madagascar. We also have not found any study of pollination in Malagasy *Erica*, but one of us (M.P.) has observed mitrastylous species flowering in the field: In contrast to those with a discoid stigma, they did not appear to release pollen into the air on disturbance, suggesting insect rather than wind pollination. Potential pollinators of these species remain to be identified. No seed information is available for Malagasy *Erica*; Perrier (1927b) suggested the seeds disperse easily and retain their viability for long periods in the soil. He also hypothesised that migratory birds may have carried *Erica* seeds between Africa, Madagascar and the Mascarenes and specifically cited overlap in the ranges of the common quail, *Coturnix coturnix*, and *Erica* in the central highlands of Madagascar (Perrier de la Bâthie 1927b).

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

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

Uses and conservation

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

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

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

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

Conclusion and research priorities

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

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

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

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

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

Appendix 1

The 35 species of *Erica* L. currently accepted in Madagascar (Antonelli et al. 2022, Elliott et al. 2024, World Flora Online 2024), with World Flora Online (WFO) and Global Biodiversity Information Facility (GBIF) identifiers and notes on distribution and ecology (unless otherwise specified, following Perrier[1]) and diagnostic traits (mostly summarised from Perrier[1]), and Perrier's[1] numbering system (#) with subsequently described species incorporated according to documented similarity. Sources: [1]Perrier (1927), [2]Dorr & Oliver (1999), [3]GBIF occurrence data (https://doi.org/10.15468/dl.pmcvqr) – see also species occurrence maps in Fig. S1.

Species	**Distribution**	**DNA data**	**Diagnostic descriptions**	**Notes**	**#**
Erica andringitrensis (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
Erica armandiana 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 *E. hebeclada* and may fall within the variation in that species.	18
Erica barnettiana 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]	
Erica baroniana 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 ("*Erica scoparia*-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
Erica betsileana (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 *E. parkeri* and *E. humbertii*, differing in habit (shrubby in *E. parkeri*) and indument (long non-glandular bristles in *E. humbertii*)	5
Erica bojeri 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 *E. hebeclada*, maybe just a variant.[1]	21

Erica bosseri Dorr https://list.worldfloraonline.org/wfo-0000671534 https://www.gbif.org/species/5682642	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 *E. madagascariensis* 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)
Erica boutonii Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000671540 https://www.gbif.org/species/5682634	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 *E. leucoclada* which has stamens fused on lower half only and broader stigmas. The var. *cinerea*[1] has greyish appearance due to denser indument.	11
Erica cryptoclada (Baker) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000671793 https://www.gbif.org/species/5682053	Central highlands, (Tsarantanana 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. *hybrida*” H.Perrier (considered synonymous[2]) found under tapia in Isalo.	30
Erica danguyana (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.	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 *E. boutonii* 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	
Erica densata 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 *E. boutonii* 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
Erica goudotiana (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 '*Philippia cauliflora gigas*', reaching 5-6 m in height) and reported 'innumerable' deviating forms.[1] Species complex.	24
Erica hebeclada Dorr & E.G.H.Oliv. https://list.worldfloraonline.	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

ARPHA Preprints Author-formatted, not peer-reviewed document posted on 12/11/2024 DOI: https://doi.org/10.3897/arphapreprints.e141580

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].	
Erica humbertii (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
Erica ibityensis (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
Erica imerinensis (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
Erica isaloensis (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

Erica jumellei (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672364 https://www.gbif.org/species/5684573	Central highlands (Arivonimamo)[1]	N	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.	Similar to *E. densata* and *E. boutonii* but leaves and flowers are smaller; sepals shorter and not split at the back (cf. *E. densata*); and with a large carinate sepal (cf. *E. boutonii*)[1].	12
Erica lecomtei (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672443 https://www.gbif.org/species/7328672	- subsp. *lecomtei*: central highlands (Ibity, Itremo)[2] - subsp. *ravinakely* Dorr: Isalo[2]	N	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.	Similar to *E. viguieri.*	28
Erica leucoclada (Baker) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672464 https://www.gbif.org/species/5684343	Central highlands (North Antsihanaka) – records also from Mandena (east coast)[3]	N	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.		13
Erica lyallii Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000672520	Central highlands (Ankaratra, Ibity)[1] –	N	See *E. baroniana.*	Considered doubtful[1]; perhaps a form of *E. baroniana* or	34(b)

https://www.gbif.org/species/5684247	records also from Kalambatritra (south)[3]			similar. *Philippia floribunda glandulosa* H. Perrier synonymous[2].	
Erica macrocalyx (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 exserted, discoid, 1 mm diam., with raised margins hiding the lobes.		15
Erica madagascariensis 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 *E. bosseri*.	1/2
Erica marojejyensis Dorr https://list.worldfloraonline.org/wfo-0000672576 https://www.gbif.org/species/5684138	Marojejy[2]	N	Distinguished from *E. lecomtei* 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 *E. lecomtei* is shorter than the corolla in length. Distinguished from *E. viguieri* 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 E. *marojejyensis* have many fewer (3 versus 9) flowers than those of *E. viguieri*.	Similar to *E. lecomtei* and *E. viguieri*[2].	28(b)
Erica minutifolia (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 *E. bojeri*; includes Perrier's concept of *E. oophylla* which	22/23

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.	
Erica myriadenia (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
Erica parkeri (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 *E. humbertii* by its glandular bristles, and adnate (as opposed to free) stamens[1].	4
Erica perhispida 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 "*Philippia hispida angustifolia*" H. Perrier from Tsaratanana unclear.[2] *Philippia adenophylla* Baker (#20) considered synonymous[2]	6/20
Erica perrieri 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					
Erica quadratiflora (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	-
Erica rakotozafyana 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
Erica spinifera (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
Erica sylvainiana 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

Erica viguieri (H. Perrier) Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000673574 https://www.gbif.org/species/5681980	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 *E. lecomtei.*	27
Erica wangfatiana Dorr & E.G.H.Oliv. https://list.worldfloraonline.org/wfo-0000673625 https://www.gbif.org/species/5681890	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 *E. baroniana*.[1]	32

516

Acknowledgements

The authors would like to thank Laurence J. Dorr and Maria S. (Bat) Vorontsova for helpful discussions in the preparation of this review. J.H. would like to thank Andry Rakotoarisoa and Franck Rakotonasolo for support and useful information, and Sami Touafchia for help with locating literature, and acknowledges funding from the Bentham-Moxon Trust for fieldwork Tsaratanana in 2022. M.P. acknowledges Dirk U. Bellstedt and E.G.H. (Ted) Oliver for collaboration, support, and funding in their joint fieldwork in 2010 and the organisers of that year's AETFAT congress for facilitating that work.

Competing interests

None declared.

References

Alm CG, Fries TCE (1927) Monographie der Gattungen *Philippia* Klotzsch, *Mitrastylus* nov. gen. und *Ericinella* Klotzsch. Kungliga svenska vetenskapsakademiens handlingar 4: 3–49.

Antonelli A, Smith RJ, Perrigo AL, Crottini A, Hackel J, Testo W, Farooq H, Torres Jiménez MF, Andela N, Andermann T, Andriamanohera AM, Andriambololonera S, Bachman SP, Bacon CD, Baker WJ, Belluardo F, Birkinshaw C, Borrell JS, Cable S, Canales NA, Carrillo JD, Clegg R, Clubbe C, Cooke RSC, Damasco G, Dhanda S, Edler D, Faurby S, de Lima Ferreira P, Fisher BL, Forest F, Gardiner LM, Goodman SM, Grace OM, Guedes TB, Henniges MC, Hill R, Lehmann CER, Lowry PP, Marline L, Matos-Maraví P, Moat J, Neves B, Nogueira MGC, Onstein RE, Papadopulos AST, Perez-Escobar OA, Phelps LN, Phillipson PB, Pironon S, Przelomska NAS, Rabarimanarivo M, Rabehevitra D, Raharimampionona J, Rajaonah MT, Rajaonary F, Rajaovelona LR, Rakotoarinivo M, Rakotoarisoa AA, Rakotoarisoa SE, Rakotomalala HN, Rakotonasolo F, Ralaiveloarisoa BA, Ramirez-Herranz M, Randriamamonjy JEN, Randriamboavonjy T, Randrianasolo V, Rasolohery A, Ratsifandrihamanana AN, Ravololomanana N, Razafiniary V, Razanajatovo H, Razanatsoa E, Rivers M, Sayol F, Silvestro D, Vorontsova MS, Walker K, Walker BE, Wilkin P, Williams J, Ziegler T, Zizka A, Ralimanana H (2022) Madagascar's extraordinary biodiversity: Evolution, distribution, and use. Science 378: eabf0869. https://doi.org/10.1126/science.abf0869

Betsch J-M (2003) Collembola, Springtails. In: Goodman SM, Benstead JP (Eds), The natural history of Madagascar. University of Chicago Press, Chicago, London, 627–638.

Boiteau P, Boiteau M, Allorge-Boiteau L (1980) Dictionnaire des noms malgaches de végétaux. Editions Alzieu.

Broothaerts N, Razanamahandry VF, Brosens L, Campforts B, Jacobs L, Razafimbelo T, Rafolisy T, Verstraeten G, Bouillon S, Govers G (2023) Vegetation changes and sediment dynamics in the Lake Alaotra region, central Madagascar. The Holocene 33: 459–470. https://doi.org/10.1177/09596836221145376

Burney DA (1987a) Late Holocene vegetational change in central Madagascar. Quaternary Research 28: 130–143. https://doi.org/10.1016/0033-5894(87)90038-X

Burney DA (1987b) Pre-settlement vegetation changes at Lake Tritrivakely, Madagascar. In: Palaeoecology of Africa and the surrounding islands. , 357–381.

Burney DA (1988) Modern pollen spectra from Madagascar. Palaeogeography, Palaeoclimatology, Palaeoecology 66: 63–75. https://doi.org/10.1016/0031-0182(88)90081-8

Carrière SM, Andrianotahiananahary H, Ranaivoarivelo N, Randriamalala J (2005) Savoirs et usages des recrus post-agricoles du pays Betsileo : valorisation d'une biodiversité oubliée à Madagascar. VertigO - la revue électronique en sciences de l'environnement 6. https://doi.org/10.4000/vertigo.3047

Crowley H (2004) Madagascar ericoid thickets. In: Burgess N, Hales J, Underwood E, Dinerstein E, Olson D, Itoua I, Schipper J, Ricketts T, Newman K (Eds), Terrestrial ecoregions of Africa and Madagascar: a conservation assessment. Island Press, 368–369.

Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, Hahn N, Palminteri S, Hedao P, Noss R, Hansen M, Locke H, Ellis EC, Jones B, Barber CV, Hayes R, Kormos C, Martin V, Crist E, Sechrest W, Price L, Baillie JEM, Weeden D, Suckling K, Davis C, Sizer N, Moore R, Thau D, Birch T, Potapov P, Turubanova S, Tyukavina A, de Souza N, Pintea L, Brito JC, Llewellyn OA, Miller AG, Patzelt A, Ghazanfar SA, Timberlake J, Klöser H, Shennan-Farpón Y, Kindt R, Lillesø J-PB, van Breugel P, Graudal L, Voge M, Al-Shammari KF, Saleem M (2017) An ecoregion-based approach to protecting half the terrestrial realm. BioScience 67: 534–545. https://doi.org/10.1093/biosci/bix014

Dorr LJ, Oliver EGH (1999) New taxa, names, and combinations in *Erica* (Ericaceae-Ericoideae) from Madagascar and the Comoro Islands. Adansonia 21: 75–91.

Elliott AC, Bester SP, Klopper RR, Nelson EC, Pirie MD (2024) Curating an online checklist for *Erica* L. (Ericaceae): contributing to and supporting global conservation through the World Flora Online. PhytoKeys 243: 121–135. https://doi.org/10.3897/phytokeys.243.121555

Fetene M, Assefa Y, Gashaw M, Woldu Z, Beck E (2006) Diversity of Afroalpine vegetation and ecology of treeline species in the Bale Mountains, Ethiopia, and the influence of fire. In: Land Use Change and Mountain Biodiversity. CRC Press, 25–38.

Gade DW, Perkins-Belgram AN (1986) Woodfuels, reforestation, and ecodevelopment in highland Madagascar. GeoJournal 12: 365–374. https://doi.org/10.1007/BF00262359

Gasse F, Van Campo E (1998) A 40,000-yr pollen and diatom record from Lake Tritrivakely, Madagascar, in the southern tropics. Quaternary Research 49: 299–311. https://doi.org/10.1006/qres.1998.1967

Gautier L, Tahinarivony JA, Ranirison P, Wohlhauser S (2018) Vegetation. In: Goodman SM, Raherilalao MJ, Wohlhauser S (Eds), The terrestrial protected areas of Madagascar: Their history, description, and biota. Association Vahatra, Antananarivo, 207–242.

Gil-Romera G, Adolf C, Benito BM, Bittner L, Johansson MU, Grady DA, Lamb HF, Lemma B, Fekadu M, Glaser B, Mekonnen B, Sevilla-Callejo M, Zech M, Zech W, Miehe G (2019) Long-term fire resilience of the ericaceous belt, Bale Mountains, Ethiopia. Biology Letters 15: 20190357. https://doi.org/10.1098/rsbl.2019.0357

Goodman SM, Benstead JP (Eds) (2004) The natural history of Madagascar. 1st ed. University of Chicago Press, Chicago, 1728 pp.

Goodman SM (Ed.) (2022) The new natural history of Madagascar. 2nd-Book Set Edition ed. Princeton University Press, Princeton, 2296 pp.

Goodman SM, Raherilalao MJ, Wohlhauser S (2018a) Site 47. Andringitra. In: The terrestrial protected areas of Madagascar: Their history, description, and biota. Association Vahatra, Antananarivo, 1044–1058.

Goodman SM, Raherilalao MJ, Wohlhauser S (2018b) Site 49. Manombo. In: The terrestrial protected areas of Madagascar: Their history, description, and biota. Association Vahatra, Antananarivo, 1070–1081.

Goodman SM, Raherilalao MJ, Wohlhauser S (2018c) Site 57. Andohahela. In: The terrestrial protected areas of Madagascar: Their history, description, and biota. Association Vahatra, Antananarivo, 1159–1179.

Grootemaat S, Wright IJ, van Bodegom PM, Cornelissen JHC (2017) Scaling up flammability from individual leaves to fuel beds. Oikos 126: 1428–1438. https://doi.org/10.1111/oik.03886

Hemp A (2006) The impact of fire on diversity, structure, and composition of the vegetation on Mt. Kilimanjaro. In: Land Use Change and Mountain Biodiversity. CRC Press, 51–67.

Joseph GS, Rakotoarivelo AR, Seymour CL (2021) How expansive were Malagasy Central Highland forests, ericoids, woodlands and grasslands? A multidisciplinary approach to a conservation conundrum. Biological Conservation 261: 109282. https://doi.org/10.1016/j.biocon.2021.109282

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA (2011) Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science 16: 406–411. https://doi.org/10.1016/j.tplants.2011.04.002

Koechlin J (1972) Flora and vegetation of Madagascar. In: Battistini R, Richard-Vindard R (Eds), Biogeography and Ecology in Madagascar. J. Cramer, Vaduz, 145–190.

Kull CA (2002) The “degraded” tapia woodlands of highland Madagascar: rural economy, fire ecology, and forest conservation. Journal of Cultural Geography 19: 95–128. https://doi.org/10.1080/08873630209478290

Kull CA, Lehmann CER (2022) Fire in highland grasslands: uses, ecology, and history. In: Goodman SM, Gautier L (Eds), The new natural history of Madagascar. Princeton University Press, 197–203.

Lehmann CER, Solofondranohatra CL, Morton JB, Phelps L, Ralimanana H, Razanatsoa J, Rakotoarimanana V, Vorontsova MS (2022) The grassy ecosystems of Madagascar. In: Goodman SM, Gautier L (Eds), The new natural history of Madagascar. Princeton University Press, 152–168.

Matsumoto K, Burney DA (1994) Late Holocene environments at Lake Mitsinjo, northwestern Madagascar. The Holocene 4: 16–24. https://doi.org/10.1177/095968369400400103

Moat J, Smith P (2007) Atlas of the vegetation of Madagascar. Royal Botanic Gardens, Kew, Richmond, Surrey, UK, 780 pp.

Musker S, Pirie M, Nürk N (2024) Worth the fuss? Maximising informativeness for target capture-based phylogenomics in *Erica* (Ericaceae). ARPHA Preprints 5: e138316. https://doi.org/10.3897/arphapreprints.e138316

Nelson EC, Pirie MD, Bellstedt DU (2024) Redefining the megagenus *Erica* L. (Ericaceae): the contributions of E. G. H. Oliver and I. M. Oliver (née Nitzsche) to taxonomy and nomenclature. PhytoKeys 244: 39–55. https://doi.org/10.3897/phytokeys.244.121705

Ojeda F (1998) Biogeography of seeder and resprouter *Erica* species in the Cape Floristic Region—Where are the resprouters? Biological Journal of the Linnean Society 63: 331–347. https://doi.org/10.1111/j.1095-8312.1998.tb01521.x

Oliver EG (2000) Systematics of Ericeae (Ericaceae: Ericoideae): species with indehiscent and partially dehiscent fruits. Contributions from the Bolus Herbarium 19.

Oliver EGH (1987) Studies in the Ericoideae (Ericaceae). VII. The placing of the genus *Philippia* into synonymy under *Erica*; the southern African species. South African Journal of Botany 53: 455–458. https://doi.org/10.1016/S0254-6299(16)31379-5

Oliver EGH (1988) Studies in the Ericoideae (Ericaceae). VI. The generic relationship between *Erica* and *Philippia* in southern Africa. Bothalia 18: 1–10. https://doi.org/10.4102/abc.v18i1.975

Oliver EGH, Forshaw N, Oliver IM, Volk F, Schumann AWS, Dorr LJ, Hoekstra RD, Musker SD, Nürk NM, Pirie MD, Rebelo AG (2024) Genus *Erica*: An identification aid version 4.00. PhytoKeys 241: 143–154. https://doi.org/10.3897/phytokeys.241.117604

Onjalalaina GE, Sattler C, Razafindravao MB, Wanga VO, Mkala EM, Mwihaki JK, Ramananirina BMR, Jeannoda VH, Hu G-W (2021) Ethnobotanical survey in Tampolo forest (Fenoarivo Atsinanana, Madagascar). https://doi.org/10.21203/rs.3.rs-153441/v1

Perrier de la Bâthie H (1921) La végétation malgache. Annales du Musée colonial de Marseille 9: 1–266.

Perrier de la Bâthie H (1927a) III Le Tsaratanana, l’Ankaratra et l’Andringitra. Académie Malgache, Tananarive, 64 pp.

Perrier de la Bâthie H (1927b) Les *Philippia* de Madagascar. In: Archives de Botanique Mémoires. Caen, 1–68.

Perrier de la Bâthie H (1934) Ericaceae et Vacciniaceae. In: Catalogue des plantes de Madagascar. Académie Malgache, Tananarive, 7–13.

Phelps LN, Andela N, Gravey M, Davis DS, Kull CA, Douglass K, Lehmann CER (2022) Madagascar's fire regimes challenge global assumptions about landscape degradation. Global Change Biology 28: 6944–6960. https://doi.org/10.1111/gcb.16206

Pirie MD, Oliver EGH, Bellstedt DU (2011) A densely sampled ITS phylogeny of the Cape flagship genus Erica L. suggests numerous shifts in floral macro-morphology. Molecular Phylogenetics and Evolution 61: 593–601. https://doi.org/10.1016/j.ympev.2011.06.007

Pirie MD, Oliver EGH, Mugrabi de Kuppler A, Gehrke B, Le Maitre NC, Kandziora M, Bellstedt DU (2016) The biodiversity hotspot as evolutionary hot-bed: spectacular radiation of *Erica* in the Cape Floristic Region. BMC Evolutionary Biology 16: 190. https://doi.org/10.1186/s12862-016-0764-3

Pirie MD, Bellstedt DU, Bouman RW, Fagúndez J, Gehrke B, Kandziora M, Maitre NCL, Musker SD, Newman E, Nürk NM, Oliver EGH, Pipins S, Niet T van der, Forest F (2024) Spatial decoupling of taxon richness, phylogenetic diversity and threat status in the megagenus Erica (Ericaceae). PhytoKeys 244: 127–150. https://doi.org/10.3897/phytokeys.244.124565

Pirie MD, Blackhall-Miles R, Bourke G, Crowley D, Ebrahim I, Forest F, Knaack M, Koopman R, Lansdowne A, Nürk NM, Osborne J, Pearce TR, Rohrauer D, Smit M, Wilman V (2022) Preventing species extinctions: A global conservation consortium for *Erica*. Plants, People, Planet 4: 335–344. https://doi.org/10.1002/ppp3.10266

Rakotoarivelo AR, Rakotoarisoa SE, de Roland L-AR, Benjara A, Rakotondratsima M, Thorstrom R, Andriambololonera S (2024) Malagasy Central Highlands: the regional perspective. In: Schneiderbauer S, Fontanella Pisa P, Shroder JF, Szarzynski J (Eds), Safeguarding Mountain Social-Ecological Systems. Elsevier, 87–96. https://doi.org/10.1016/B978-0-443-32824-4.00038-9

Ralimanana H, Perrigo AL, Smith RJ, Borrell JS, Faurby S, Rajaonah MT, Randriamboavonjy T, Vorontsova MS, Cooke RSC, Phelps LN, Sayol F, Andela N, Andermann T, Andriamanohera AM, Andriambololonera S, Bachman SP, Bacon CD, Baker WJ, Belluardo F, Birkinshaw C, Cable S, Canales NA, Carrillo JD, Clegg R, Clubbe C, Crottini A, Damasco G, Dhanda S, Edler D, Farooq H, de Lima Ferreira P, Fisher BL, Forest F, Gardiner LM, Goodman SM, Grace OM, Guedes TB, Hackel J, Henniges MC, Hill R, Lehmann CER, Lowry PP, Marline L, Matos-Maraví P, Moat J, Neves B, Nogueira MGC, Onstein RE, Papadopulos AST, Perez-Escobar OA, Phillipson PB, Pironon S, Przelomska NAS, Rabarimanarivo M, Rabehevitra D, Raharimampionona J, Rajaonary F, Rajaovelona LR, Rakotoarinivo M, Rakotoarisoa AA, Rakotoarisoa SE, Rakotomalala HN, Rakotonasolo F, Ralaiveloarisoa BA, Ramirez-Herranz M, Randriamamonjy JEN, Randrianasolo V, Rasolohery A, Ratsifandrihamanana AN, Ravololomanana N, Razafiniary V, Razanajatovo H, Razanatsoa E, Rivers M, Silvestro D, Testo W, Torres Jiménez MF, Walker K, Walker BE, Wilkin P, Williams J, Ziegler T, Zizka A, Antonelli A (2022) Madagascar's extraordinary biodiversity: Threats and opportunities. Science 378: eadf1466. https://doi.org/10.1126/science.adf1466

Randriatsara FO (2014) Rôles et importances écologiques du feu sur la dynamique des savanes dans la Réserve Spéciale d'Ambohitantely, Hautes Terres Centrales de Madagascar. Mémoire en vue de l'obtention du diplôme d'études approfondies (DEA) en foresterie, dévéloppement et environnement. Université d'Antananarivo

Rasolonandrasana B, Grenfell S (2003) Parc National d'Andringitra. In: Goodman SM, Benstead JP (Eds), The natural history of Madagascar. University of Chicago Press, Chicago, London, 1489–1494.

Ratsirarson J, Edwards ME, Olsson EGA, Ambruster WS, Pareliussen I, Réau B (2003) Forest restoration and biodiversity conservation in the central highlands: the case of the Réserve Spéciale d'Ambohitantely. In: Goodman SM, Benstead JP (Eds), The natural history of Madagascar. University of Chicago Press, Chicago, London, 1472–1480.

Razafimanantsoa AHI (2022) Holocene vegetation history and environmental change in the forest-grassland mosaic of the Central Highlands of Madagascar. Doctoral thesis. University of Cape Town Available from: http://hdl.handle.net/11427/36720 (October 23, 2024).

Razafimanantsoa AHI, Razanatsoa E (2024) Modern pollen rain reveals differences across forests, open and mosaic landscapes in Madagascar. Plants, People, Planet 6: 729–742. https://doi.org/10.1002/ppp3.10487

Reinhardt AL, Kasper T, Lochner M, Bliedtner M, Krahn KJ, Haberzettl T, Shumilovskikh L, Rahobisoa J-J, Zech R, Favier C, Behling H, Bremond L, Daut G, Montade V (2022) Rain forest fragmentation and environmental dynamics on Nosy Be island (NW Madagascar) at 1300 cal BP is attributable to intensified human impact. Frontiers in Ecology and Evolution 9: 783770. https://doi.org/10.3389/fevo.2021.783770

Sarwar AKMG, Takahashi H (2014) Pollen morphology of *Erica* L. and related genera and its taxonomic significance. Grana 53: 221–231. https://doi.org/10.1080/00173134.2014.912346

Schatz GE (2005) Generic tree flora of Madagascar. Royal Botanic Gardens Kew, Kew, 492 pp.

Silander Jr. JA, Bond WJ, Ratsirarson J (2024) The grassy ecosystems of Madagascar in context: Ecology, evolution, and conservation. Plants, People, Planet 6: 94–115. https://doi.org/10.1002/ppp3.10417

Solofondranohatra CL, Vorontsova MS, Hackel J, Besnard G, Cable S, Williams J, Jeannoda V, Lehmann CER (2018) Grass functional traits differentiate forest and savanna in the Madagascar central highlands. Frontiers in Ecology and Evolution 6. https://doi.org/10.3389/fevo.2018.00184

Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Straka H (1991) Palynologia madagassica et mascarenica. 2. Echantillons de surface. Adademie der Wissenschaften und der Literatur, Mainz.

Straka H (1996) Histoire de la végétation de Madagascar oriental dans les derniers 100 millénaires. In: Lourenço WR (Ed.), Biogéographie de Madagascar. ORSTOM éditions, Paris, 37–47.

Straka H (2001) Palynologia madagassica et mascarenica III. Sur l'histoire tardiglaciaire de la végétation de la partie orientale de Madagascar et des Mascareignes. Le Journal de Botanique 13: 47–88. https://doi.org/10.3406/jobot.2001.1826

Vences M, Wollenberg KC, Vieites DR, Lees DC (2009) Madagascar as a model region of species diversification. Trends in Ecology & Evolution 24: 456–465. https://doi.org/10.1016/j.tree.2009.03.011

Verdaguer D, Ojeda F (2002) Root starch storage and allocation patterns in seeder and resprouter seedlings of two Cape *Erica* (Ericaceae) species. American Journal of Botany 89: 1189–1196. https://doi.org/10.3732/ajb.89.8.1189

Vernier E (1964) Étude sur la fabrication des Lambamena. Journal des Africanistes 34: 7–34. https://doi.org/10.3406/jafr.1964.1377

de Veyrières P, de Méritens G (1967) Le livre de la sagesse malgache : proverbes, dictons, sentences, expressions figurées et curieuses. Éditions Maritimes et d'Outre-mer, Paris, 663 pp.

Virah-Sawmy M (2009) Ecosystem management in Madagascar during global change. Conservation Letters 2: 163–170. https://doi.org/10.1111/j.1755-263X.2009.00066.x

Virah-Sawmy M, Gillson L, Willis KJ (2009a) How does spatial heterogeneity influence resilience to climatic changes? Ecological dynamics in southeast Madagascar. Ecological Monographs 79: 557–574. https://doi.org/10.1890/08-1210.1

Virah-Sawmy M, Willis KJ, Gillson L (2009b) Threshold response of Madagascar's littoral forest to sea-level rise. Global Ecology and Biogeography 18: 98–110.

https://doi.org/10.1111/j.1466-8238.2008.00429.x

Wesche K (2006) Is Afroalpine plant biodiversity negatively affected by high-altitude fires? In: Land Use Change and Mountain Biodiversity. CRC Press, 39–49.

World Flora Online (2024) *Erica* L. Available from: http://www.worldfloraonline.org/taxon/wfo-4000013772 (September 30, 2024).

Wrońska-Pilarek D, Szkudlarz P, Bocianowski J (2018) Systematic importance of morphological features of pollen grains of species from *Erica* (Ericaceae) genus. PLOS ONE 13: e0204557. https://doi.org/10.1371/journal.pone.0204557

Zizka A, Andermann T, Silvestro D (2022) IUCNN – Deep learning approaches to approximate species' extinction risk. Diversity and Distributions 28: 227–241. https://doi.org/10.1111/ddi.13450

Zizka A, Silvestro D, Andermann T, Azevedo J, Duarte Ritter C, Edler D, Farooq H, Herdean A, Ariza M, Scharn R, Svantesson S, Wengström N, Zizka V, Antonelli A (2019) CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. Methods in Ecology and Evolution 10: 744–751. https://doi.org/10.1111/2041-210X.13152

808 **Figures**

809

Figure 1: Floral diversity of *Erica* in Madagascar. A selection of specimens collected by E.G.H. Oliver and colleagues: A. *E. bojeri* (EO12649); B. *E. boutonii* Dorr & E.G.H.Oliv. (EO12676); C. *E. cryptoclada* (Baker) Dorr & E.G.H.Oliv. (EO12642); D. *E. hebeclada* Dorr & E.G.H.Oliv. (EO12690); E. *E. humbertii* (H.Perrier) Dorr & E.G.H.Oliv. (EO12648); F. *E. myriadenia* (Baker) Dorr & E.G.H.Oliv. (EO12677); G. *E. parkeri* (EO12626); H. *E. perrieri* (EO12635); I. *E. rakotozafyana* Dorr & E.G.H.Oliv. (EO12681). Photos: Michael D. Pirie.

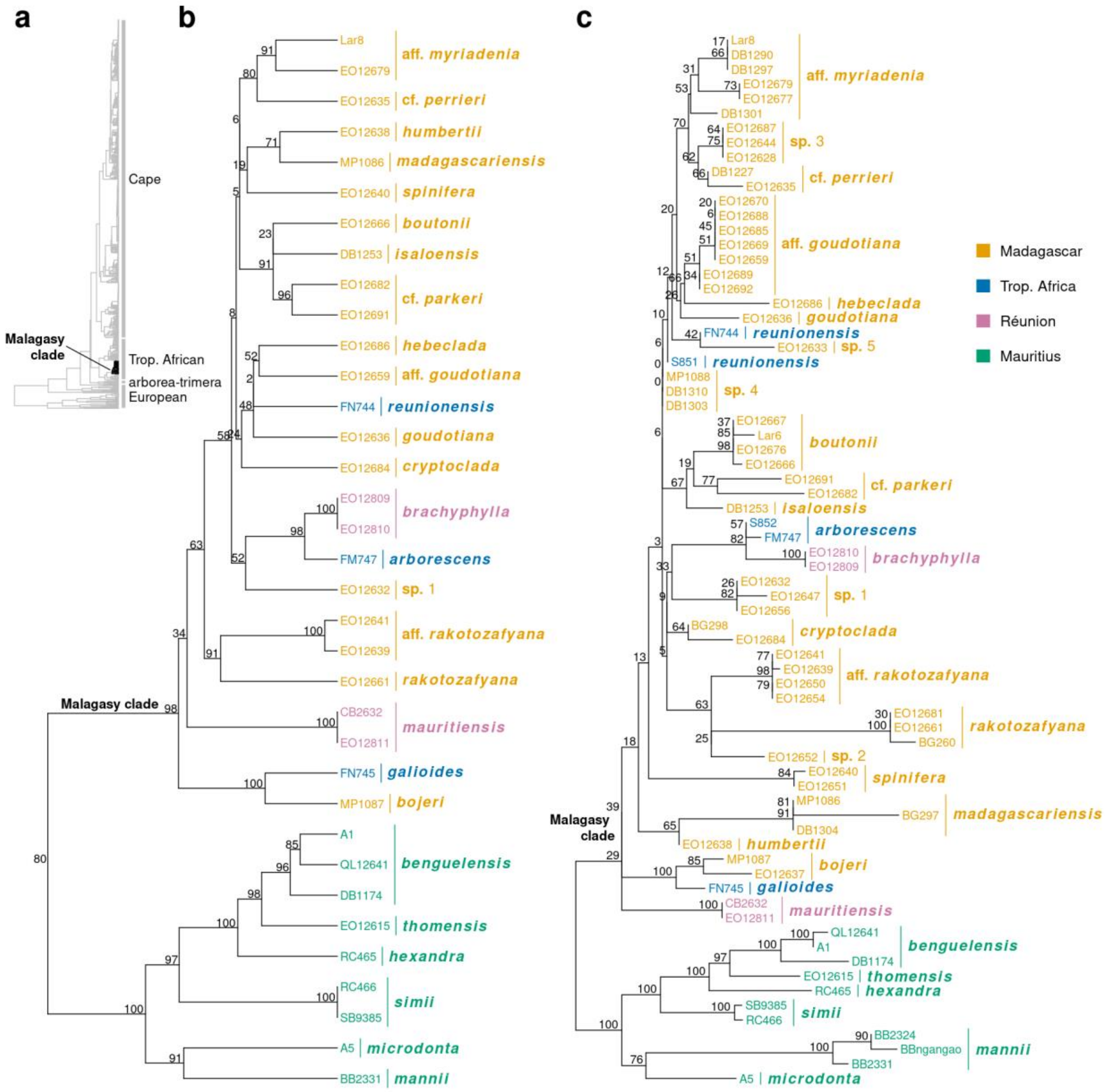

Figure 2: Phylogenetic relationships of Malagasy *Erica*. (a) Position of the Malagasy clade in the genus according to (Pirie et al. 2024). The tree includes 771 accessions and several nuclear and plastid markers. (b) Focus on the Malagasy clade and its Tropical African sister clade (same tree as in a). (c) Tree estimated from the same marker set as in a-b but expanded with ITS for 36 additional accessions. Values on nodes are Felsenstein bootstrap support percentages.

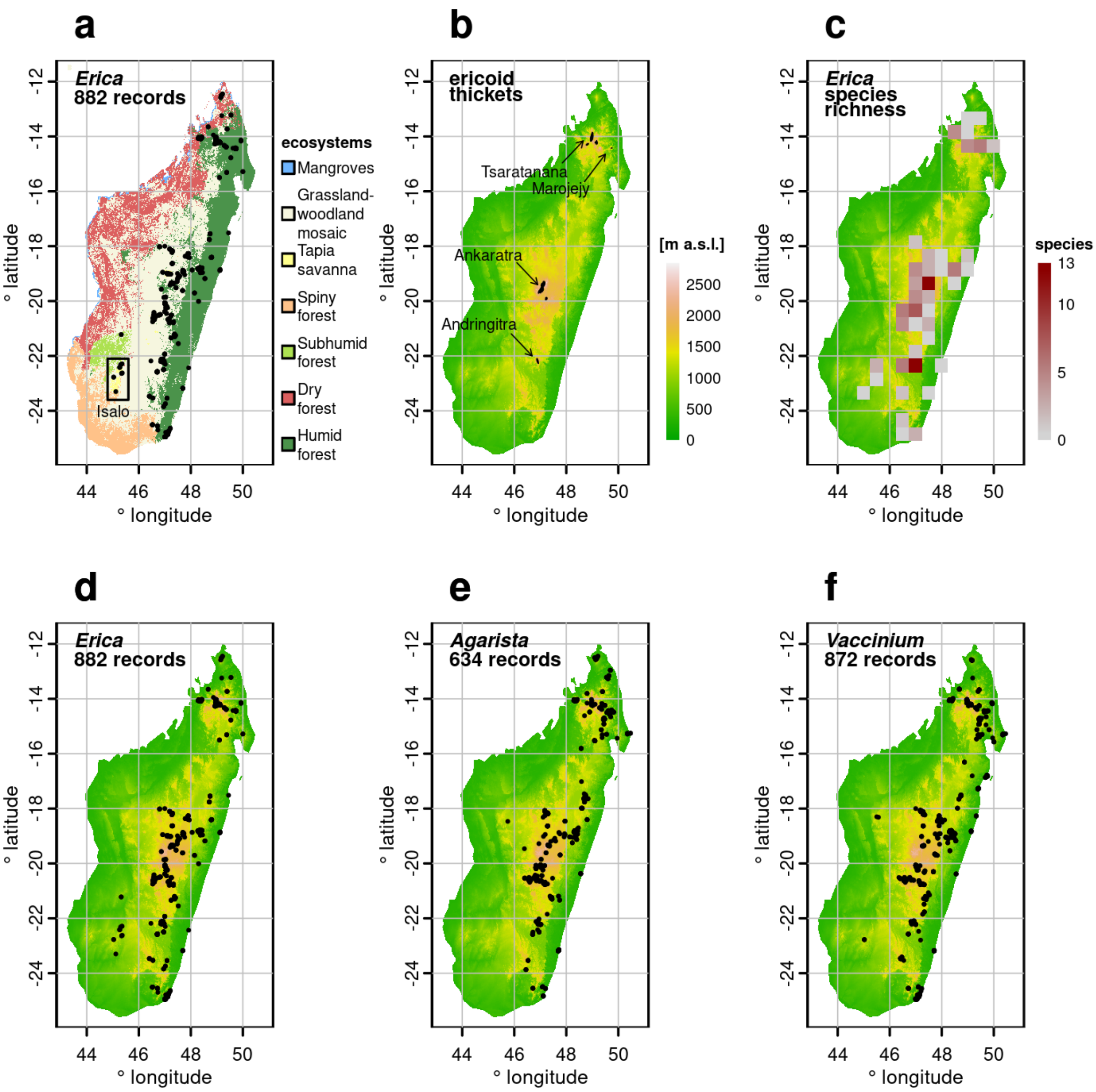

Figure 3: Distribution of *Erica* and other Ericaceae in Madagascar. Occurrence data were obtained from the Global Biodiversity Information Facility and submitted to multiple filtering steps (see text). (a) *Erica* distribution plotted against the Madagascar ecosystem map of (Antonelli et al. 2022).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

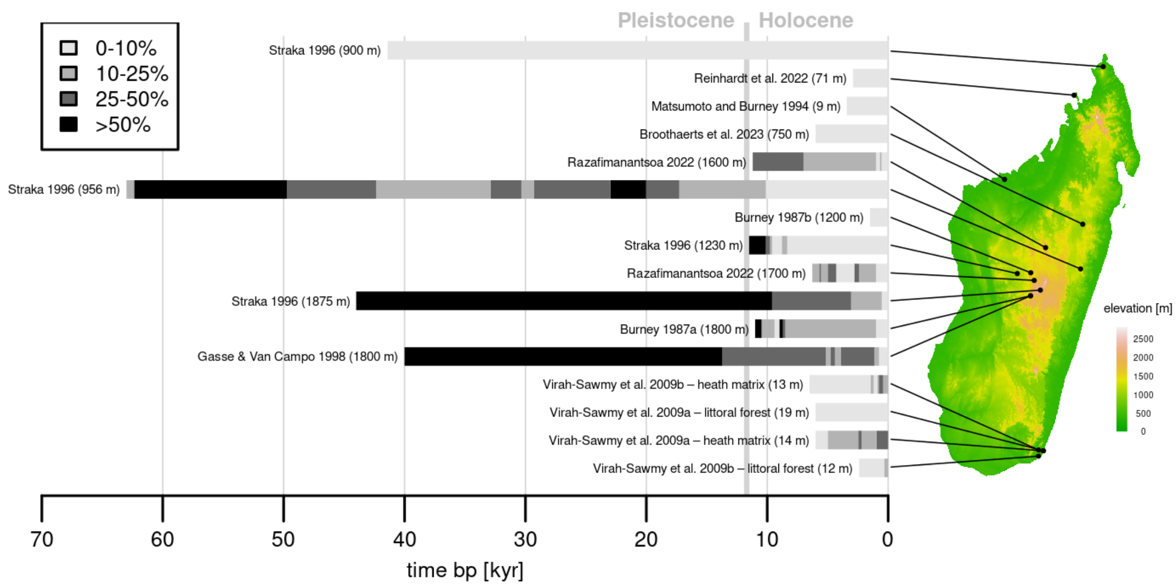

Figure 4: Habitats and uses of *Erica* in Madagascar. (a) *Erica* sp. in a mosaic with grassland, Andringitra National Park, Southeast, c. 2,000 m elevation. Lorna MacKinnon, Diana Rabeharison, Nantenaina Rakotomalala, and Fenitra Randrianarimanana 2022. (b) *Erica* sp. on coastal sand, Manombo Special 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.

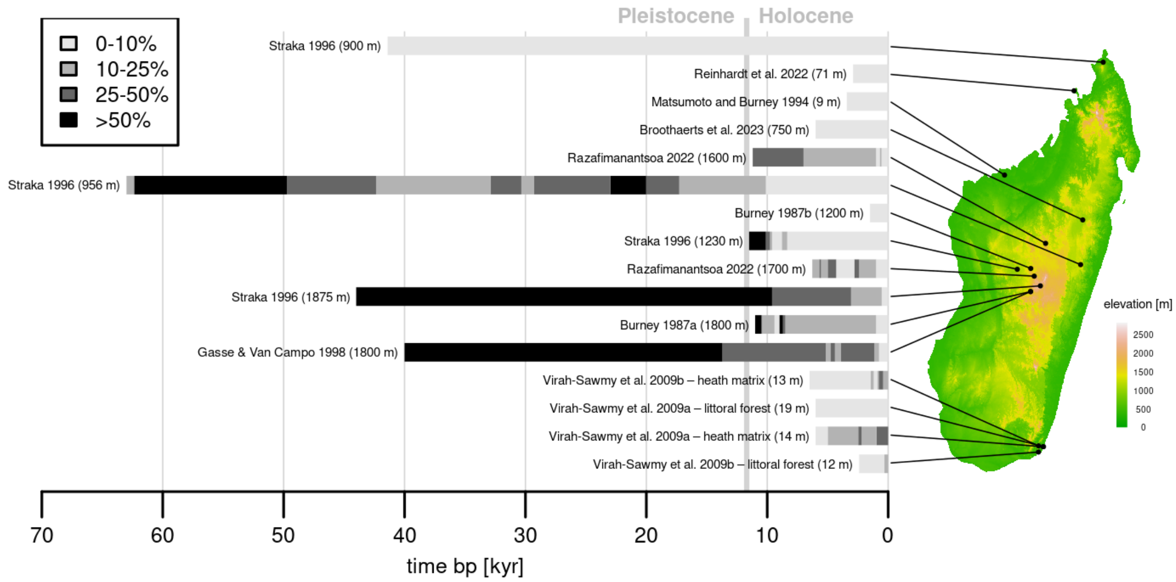

Figure 5: Abundance of Ericaceae pollen over time as proportion of overall pollen counts in sediment chronosequences in Madagascar. Data shown were summarised manually from 11 studies that recorded Ericaceae (see table S2), varying in temporal extent and resolution. Only one study (Virah-Sawmy 2009b) 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.

ARPHA Preprints Author-formatted, not peer-reviewed document posted on 12/11/2024. DOI: https://doi.org/10.3897/arphapreprints.e141580

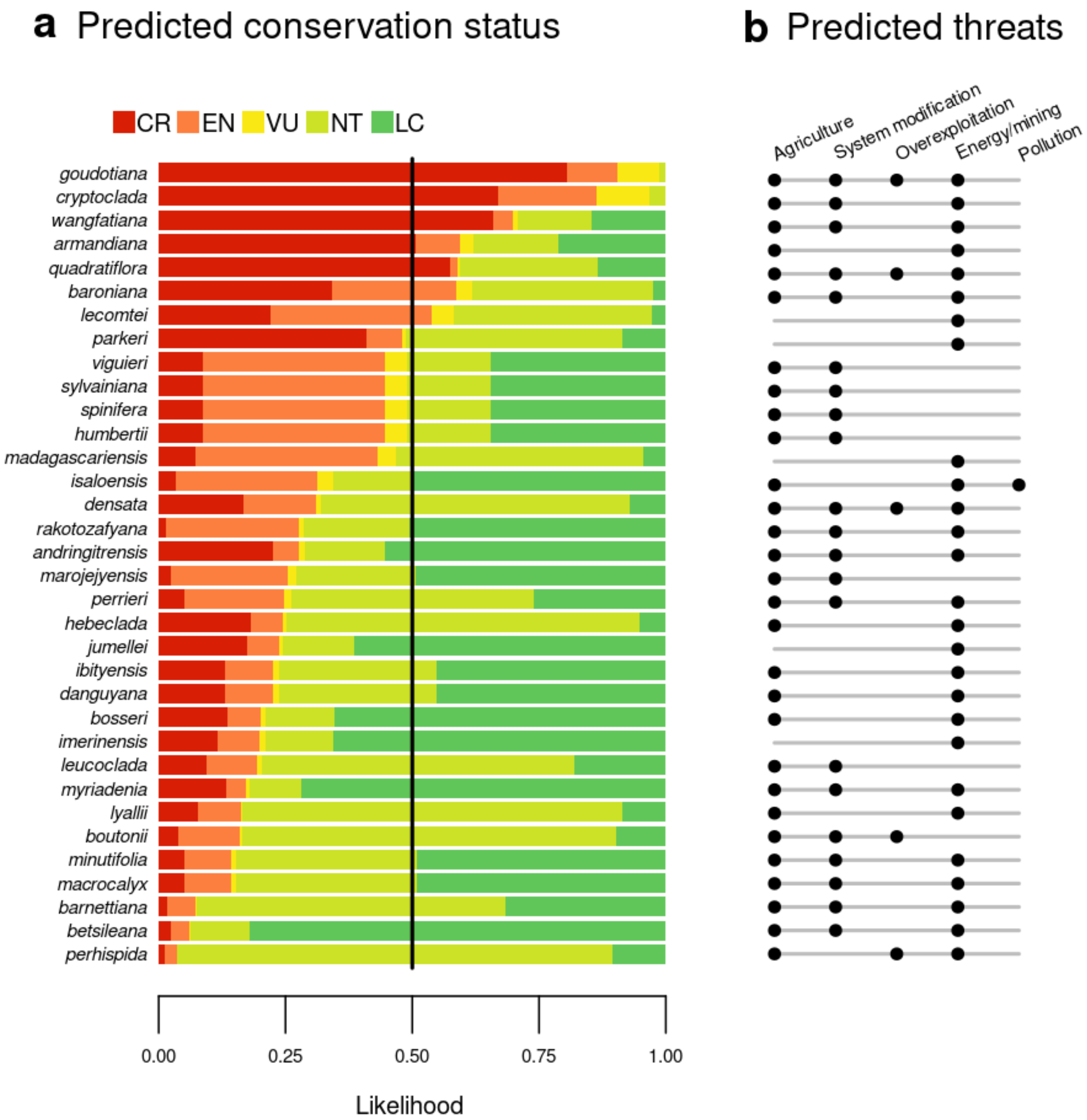

Figure 6: Predicted conservation status and threats for Malagasy *Erica* species, from Ralimanana et al. (2022). International Union for the Conservation of Nature categories for (a) conservation status and (b) threats were predicted for all unassessed plant species of Madagascar using a neural network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

Supplementary Material

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

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

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