

Article

Ancient Plant Lineages Endemic to Africa and Its Islands: An Analysis on the Distribution and Diversity

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Abstract: Although Africa and Madagascar host numerous endemic plant families and genera, there has been no attempt to use recent phylogenies in order to summarise information on their age or map their distribution and diversity. Here, we list 35 plant lineages endemic to Africa and its islands deemed to be older than 100 Mya, map their distribution, richness, and weighted endemism, and discuss intrinsic and extrinsic factors that may have facilitated their survival. High concentrations of ancient endemic lineages are found in the Cape and more broadly across southern Africa, in the Congolian rainforests, but also in East Africa and Madagascar, these last two areas sharing surprisingly many lineages. Africa and its islands host a highly distinctive assemblage of unique plant lineages, adapted to humid, mesic, dry, and in several cases fire-prone, environments. A better understanding of their history and ecology will facilitate their conservation in a changing climate.

Keywords: Africa; Cape; endemism; Madagascar; phylogenetic endemism



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1. Introduction

Antiquity has become an important key concept and consideration in conservation science. On the one hand, the use of phylogenetic diversity in conservation planning places greater weight on lineages that have been separated from other living lineages for a longer period of time [1,2]. On the other hand, the term ‘ancient’ in itself resonates deeply with the general public [3], and as such is used as a catch word in conservation marketing. The antiquity of biotic lineages is often quoted as evidence of prolonged survival in situ, of the antiquity of a flora as a whole, or even of the antiquity of the vegetation types where the lineages live, although these aspects are not necessarily linked. Biotic lineages may persist in dramatically changing vegetation or disperse outside the area of origin and only survive in their newly adoptive region [4].

Most continents preserve and house some ancient plant lineages, and the outcome of comparisons between continents depends on the precise taxa under consideration, and on the methods used [5]. Much has been written about southern/Gondwanan floras and their changes through geological epochs (e.g., [6]), and this literature is valuable in understanding African plant life and its paleo-floristic linkages. However, as with all paleontological studies, this type of work is biased in favour of the dominant taxa, and likely to miss lineages that were rare and localized through much of their evolutionary history. Recent phylogenies [7] tend to push back the origins of angiosperm families much further into the past than previously thought, which may point to the incompleteness of the fossil record.

Tropical African flora have already been studied taking into consideration phylogenetic pattern [8]. However, this assessment did not attempt to highlight the specific ancient lineage characteristics of the region. It also did not include the Indian Ocean islands or the southern tip of the continent, considered to harbor distinct flora despite their proximity. Here, we attempt to fill these gaps.

2. Materials and Methods

The Angiosperm Phylogeny Website (APWeb) [9] was scrutinised for lineages restricted to Africa and/or its islands. The stem ages of these lineages were then derived from the phylogeny of Janssens et al. [7], and lineages older than 100 Mya (million years ago, mid-Cretaceous) were retained. A more recent cut-off value would have been preferable for including a greater array of lineages. However, it was found that the age disagreement between the Janssens et al. [7] tree and group-specific trees quoted in APWeb [9] was substantially increased for nodes below this value, not just in terms of absolute values, but also proportionally. This would have meant that the palaeoecological significance of the group of selected lineages would have been largely compromised. Lineages not included in the Janssens et al. [7] tree were included here if their positioning in group-specific phylogenies, or the proportionality between their stem age and the age of the node immediately older therein, implied an age older than 100 Mya by Janssens et al. [7] standards.

The ages of gymnosperm lineages in most recent phylogenies are not well aligned with angiosperm ages as calculated by Janssens et al. [7]. However, excluding gymnosperms from our study would have been a major gap. One study including most major gymnosperm lineages, as well as a fair selection of angiosperms is that of Liu et al. [10]. One node from this study (the separation of Proteales from the superrosids), comparable in age with many relevant gymnosperm lineages, was used to calculate ages for gymnosperms that are compatible with Janssens et al. [7] by proportionality with the values of the latter. It should be noted that, although the resulting values are substantially higher than the best estimates in Liu et al. [10], they do nevertheless fall within the error bars presented in that study.

Where one endemic ancient lineage included two or more sub-lineages older than 100 Mya, the group was counted as one lineage.

The distributions of lineages were mapped using maps from APWeb [9], as well as research-grade records from iNaturalist (2023) [11], records from [12] Encyclopedia of Life (2023) and references therein and using the ecoregions of [13] Olson et al., (2001) as geographic units for analysis (Supplementary Data Table S1). The diversity of ancient lineages (viz. lineage richness) and weighted endemism of ecoregions were mapped with ArcGIS version 10.8 [14]. Weighted endemism was calculated by dividing the presences of lineages in geographic units by the square of the number of units where each lineage is present, before summing them up [5].

3. Results

Thirty-five lineages endemic to Africa and/or its islands were retained as likely older than 100 Mya. These included three gymnosperms (*Stangeria*, *Encephalartos* and *Welwitschia*), one paleodicot (*Hypodaphnis*), six monocots, and 25 eudicots lineages. The oldest lineage retained here is *Didymeles*, endemic to Madagascar, which split from core Buxaceae 170 Mya, while, at the other end of the age spectrum, *Lichtensteinia* split from other Apiaceae 103 Mya, and *Encephalartos* from *Lepidozamia* 101 Mya. Thirteen of the included lineages are classified as genera within more widespread higher taxa, one as a group of genera (the African Tecophileaceae, was retrieved as monophyletic by Janssens et al. [7] but with no taxonomic rank assigned), one as a subfamily (Iridaceae: Nivenioideae, including *Nivenia*, *Klattia* and *Witsenia*), twenty-one as families (with one or more genera), and the Bruniales as a fully fledged order (Table 1). Single-genus lineages are referred to further down at the genus level, even if recognised as families; lineages with multiple genera in the same (sub)family are referred to at that respective level.

Table 1. Ancient lineages endemic to Africa and/or its islands, and their taxonomic placement. Most lineages are endemic at either genus or family level, while the Bruniales is endemic as an entire order (indicated by shading).

Lineage Number	Order	Family	Genus/Genera	Species	Age (Mya)	Distribution
1	Cycadales	Zamiaceae	<i>Stangeria</i>	1	149	SE Africa
2	Cycadales	Zamiaceae	<i>Encephalartos</i>	68	101	much of Africa, mostly SE
3	Welwitschiales	Welwitschiaceae	<i>Welwitschia</i>	1	168	SW Africa
4	Laurales	Lauraceae	<i>Hypodaphnis</i>	1	112	W Africa
5	Asparagales	Lanariaceae	<i>Lanaria</i>	1	131	Cape
6	Asparagales	Amaryllidaceae	<i>Agapanthus</i>	8	124	southern Africa
7	Asparagales	Iridaceae	<i>Nivenia</i> , <i>Klattia</i> , <i>Witsenia</i>	14	103	Cape
8	Asparagales	Iridaceae	<i>Aristea</i>	55	113	much of Africa, Madagascar
9	Asparagales	Tecophileaceae	<i>Cyanastrum</i> , <i>Cyanella</i> , <i>Kabuyea</i> , <i>Walleria</i>	16	119	much of Africa
10	Asparagales	Aparagaceae	<i>Eriospermum</i>	114	120	much of Africa, mostly Cape
11	Dioscoreales	Afrothismiaceae	<i>Afrothismia</i>	16	123	central Africa
12	Buxales	Buxaceae	<i>Didymeles</i>	2	170	Madagascar
13	Gunnerales	Myrothamnaceae	<i>Myrothamnus</i>	2	168	southern and East Africa, Madagascar
14	Saxifragales	Peridiscaceae	<i>Medusandra</i>	2	137	central Africa
15	Rosales	Dirachmaceae	<i>Dirachma</i>	2	104	Horn of Africa, Socotra
16	Oxalidales	Huaceae	<i>Afrostyrax</i> , <i>Hua</i>	4	151	central and W Africa
17	Myrtales	Combretaceae	<i>Strephonema</i>	2	109	central and W Africa
18	Crossosomatales	Aphloiaceae	<i>Aphloia</i>	1	146	southern and East Africa, Madagascar
19	Malvales	Sphaerosepalaceae	<i>Dialyceras</i> , <i>Rhopalocarpus</i>	18	130	Madagascar
20	Brassicales	Pentadiplandraceae	<i>Pentadiplandra</i>	1	109	central Africa
21	Huerteales	Gerrardinaceae	<i>Gerrardina</i>	2	148	southern and East Africa
22	Sapindales	Kirkiaceae	<i>Kirkia</i>	8	106	southern and East Africa, Madagascar
23	Santalales	Octoknemaceae	<i>Octoknema</i>	14	117	central and W Africa
24	Caryophyllales	Asteropeiaceae, Physenaceae	<i>Asteropeia</i> , <i>Physena</i>	10	121	Madagascar
25	Caryophyllales	Kewaceae	<i>Kewa</i>	6	137	southern Africa, mostly Cape
26	Caryophyllales	Barbeuiaceae	<i>Barbeuia</i>	1	124	Madagascar
27	Caryophyllales	Didiereaceae	<i>Portulacaria</i> , <i>Calyptrotheca</i> , <i>Alluaudia</i> , <i>Alluaudiopsis</i> , <i>Decarya</i> , <i>Didierea</i>	20	113	southern and East Africa, Madagascar
28	Cornales	Hydrostachydaceae	<i>Hydrostachys</i>	21	103	southern and East Africa, Madagascar
29	Cornales	Curtisiaceae, Grubbiaceae	<i>Curtisia</i> , <i>Grubbia</i>	4	110	southern and East Africa
30	Ericales	Sladeniaceae	<i>Ficalhoa</i>	1	143	southern and East Africa
31	Ericales	Roridulaceae	<i>Roridula</i>	2	132	Cape

Table 1. Cont.

Lineage Number	Order	Family	Genus/Genera	Species	Age (Mya)	Distribution
32	Asterales	Rousseaceae	<i>Roussea</i>	1	135	Mauritius
33	Bruniales	Bruniaceae	<i>Audouinia</i> , <i>Berzelia</i> , <i>Brunia</i> , <i>Linconia</i> , <i>Staaavia</i> , <i>Thamnea</i>	81	152	southern Africa, mostly Cape
34	Apiales	Apiaceae	<i>Lichtensteinia</i>	7	103	southern Africa, mostly Cape
35	Solanales	Convolvulaceae	<i>Humbertia</i>	1	132	Madagascar

A large proportion of the lineages were represented by single species, or by pairs of species. Nevertheless, some (*Eriospermum*, *Encephalartos*, *Aristea*, Bruniales) comprise substantial radiations, with more than 50 species each. In most cases, however, multi-species lineages are represented by fully allopatric species, meaning that at any given locality a single species per lineage is present. There are, however, exceptions, such as the Bruniales, where species are highly differentiated into narrow niches, as is the case with other, more recent, lineages associated with Cape fynbos vegetation.

The endemic lineages were separated neatly between a rainforest group (*Hypodaphnis*, *Afrothismia*, *Medusandra*, Huaceae, *Strephonema*, *Pentadiplandra*, *Octoknema*) and a second group ranging across arid, semi-arid and seasonally dry environments, which formed a continuum between the Cape (*Lanaria*, Iridaceae: *Nivenioideae*, *Roridula*), elsewhere in southern Africa (*Stangeria*, *Welwitschia*), southern Africa including the Cape (*Agapanthus*, *Kewia*, Bruniaceae, *Lichtensteinia*), southern and East Africa (*Curtisia* + *Grubbia*, and arguably *Ficalhoa*), southern Africa to Madagascar (*Myrothamnus*, *Aphloia*, *Kirkia*, *Didiereaceae*, *Hydrostachys*), Madagascar only (*Didymeles*, *Sphaerosepalaceae*, *Asteropeia* + *Physena*, *Barbeuia*, *Humbertia*) and the Mascarenes (*Roussea*). There are also a handful of lineages widespread through continental Africa (*Encephalartos*, *Eriospermum*, African Tecophileaceae), in one case including Madagascar (*Aristea*). *Dirachma* alone is endemic to the horn of Africa (*Barbeya*, also in Rosales, is not included here as it also occurs in the Arabian Peninsula, as do the more widespread mainly African Stilbaceae). The Tecophileaceae were the only lineage including species ranging from the Congolian rainforest, across semi-arid ecosystems, all the way to the Cape fynbos.

Lineages that narrowly missed the 100 Mya age cutoff included several paleodicty (e.g., *Takhtajania*), monocots (e.g., *Tulbaghia*, *Kniphofia*) and eudicots (e.g., *Geissolomataceae*, *Penaeeaceae*, *Protea*), while other lineages referred to as ancient in various contexts (such as the African, Malagasy Mascarene and Seychelles *Arecaceae*, and even endemic families such as the *Sarcolenaceae*) missed inclusion by a larger margin.

A somewhat surprising lineage retrieved here as older than 100 Mya, and with sampled genera coming solely from Africa, is *Greyia* + *Melianthus* + *Bersama*, sister to the South American *Viviania*, spanning two families in Geraniales. The position of *Viviania* outside the clade of African taxa is contrary to the accepted familial classification [15], and suggests the possibility of a need for taxonomic reshuffle in this angiosperm order. However, due to the absence of the South American *Francoa* from the tree, we do not include this lineage in the analyses, as *Francoa* may yet fall within the otherwise African clade and thus negate its endemic status, while *Melianthus* + *Bersama* alone would not meet the age criterion.

The highest diversity of ancient endemic lineages was reached in the Cape (especially in Montane Fynbos), with high values also noted throughout the rest of southern and East Africa, and with secondary hotspots in Madagascar, and Central Africa (the Atlantic Equatorial forests of Gabon and the Cross-Sanaga-Bioko forests centered in western Cameroon) (Figure 1A). Endemism shows similar patterns, but with an even greater concentration of the top values in Montane Fynbos, eastern Madagascar, and Central Africa, and less pronounced in East Africa (Figure 1B).

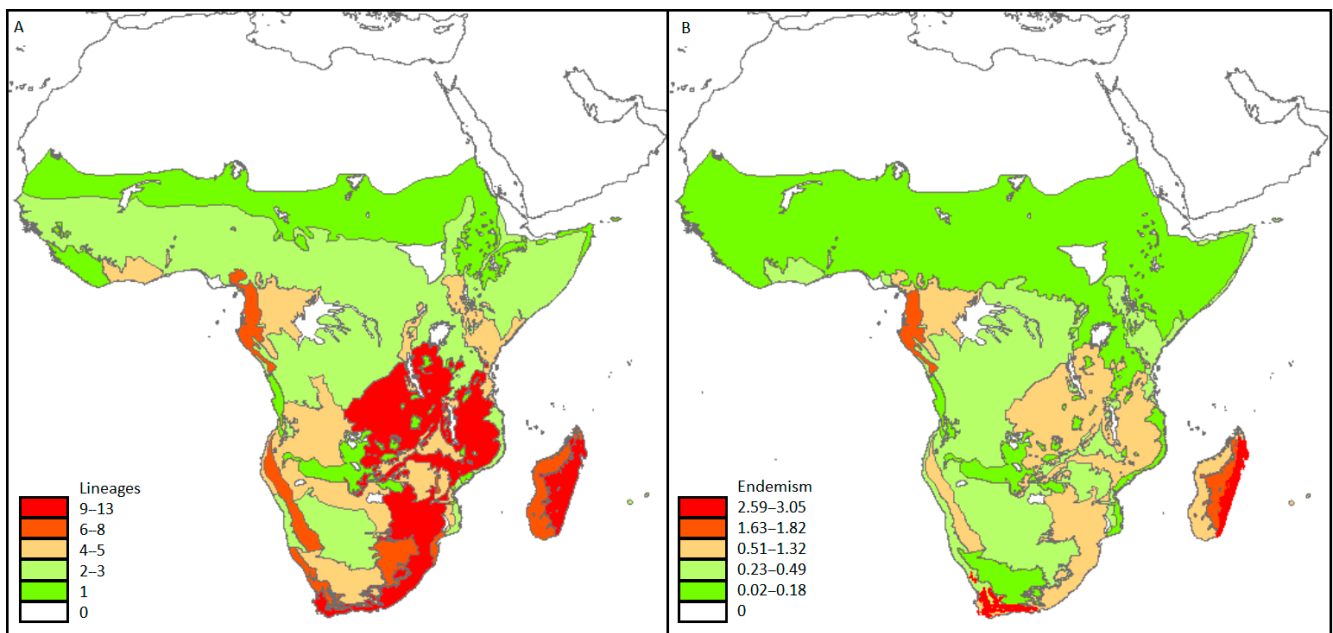


Figure 1. The richness (A) and endemism (B) of ancient lineages endemic to Africa and its islands.

4. Discussion

The lineage ages in the Janssens et al. [7] trees are substantially older (in some cases twice so!) than those in earlier angiosperm phylogenies, whether comprehensive or group specific. It can be argued that these new values are likely to be overestimates, and as such they may bias the picture presented here. A perusal of the ages indicated in APWeb [9], derived from group-specific phylogenies, suggests that, with an adjustment of the cut-off ages (ca. 50 Mya instead of 100 Mya), a very similar set of lineages is derived. This would likely exclude (depending on the precise algorithm of selection, as in some cases APWeb [9] provides more than one age value) the Asparagales, Solanales and, Caryophyllales lineages included here, but additionally include *Napoleonaea* (Lecythidaceae) and the Siphonochiloideae (Zingiberaceae), as well as some further lineages in Apiaceae and Malvales. The data set thus assembled would be at least 60% similar to the current one used here, and the differentiating lineages would in turn have distributions largely similar to those they replace. Consequently, we will contend that the geographic patterns presented here are reasonably representative for a set of ancient lineages of this size, although the different ages implied by using older phylogenetic studies would have somewhat different implications in terms of the lineages' paleoecology and dispersal pathways.

Peak values in Central Africa, Madagascar and the Cape are in line with our general understanding of plant diversity patterns in Africa as derived from global studies [16], while the high values in East Africa, and the large number of ancient lineages shared between East Africa and Madagascar have perhaps not been highlighted sufficiently in the past. If taking species richness as a null model against which ancient lineage diversities are to be discussed, East Africa and the western, drier parts of Madagascar, stand out. The continuum between the Cape and Madagascar, via East Africa, highlights the importance of considering Africa as a whole in assessments of ancient endemism (cf. [8]).

To better understand these patterns, it is important to discuss the environmental correlates of the groups listed here. The present-day climate has been used to predict plant diversity patterns, however, past climates are more important in the context of ancient lineage diversity. Both the Cape [17] and the Guineo-Congolian-Madagascar continuum, including East Africa [18], have been highlighted as areas of high past climatic stability, albeit over different time frames. Perhaps the most important aspect when relating the distribution of ancient lineages to environmental factors is water availability. The Central- and West- African ancient endemics are typically rainforest lineages and represent

a fair proportion of our dataset. This is in line with the predominance of mesophytic lineages in the grade leading to the eudicots [7], which may suggest a mesophytic origin for the angiosperms and may lead to an expectation that ancient lineages would mostly belong in the humid tropics. Nevertheless, many of the ancient lineages endemic to Africa are not mesophytes; in fact, a substantial proportion are highly adapted to aridity or seasonal drought (*Welwitschia*, *Myrothamnus*, *Kewia*, Didiereaceae). While *Kewia* and the Didiereaceae are succulents (and the latter are locally dominant in SE South Africa and SW Madagascar) [19], the most diverse succulent groups present in Africa (*Euphorbia*, Aizoaceae) have evolved more recently [7]. Likewise, proper geophytism is more recent, with the ancient lineages in Asparagales endemic to Africa being shrubby or rhizomatous (cf. [20]). In contrast, *Welwitschia* and *Myrothamnus* have different, unique adaptations to water scarcity.

A second environmental factor to be considered is fire. The highest diversity of ancient lineages in fire-driven Montane Fynbos in the Cape is remarkable, given the fact that this region is best known for its recent diversification [1]. An ancient endemic-rich Cape is reminiscent of Tasmania's paleoendemics, many of which are adapted to fire-prone environments [21]. However, the lineages currently dominant in Montane Fynbos thanks to their fire adaptations (*Erica*, the African Restionaceae and two Proteaceae lineages) are actually more recent.

The more recent origin of the adaptations to the seasonally dry, fire-prone, nutrient-poor Cape environments is also illustrated by lineages only partly represented by Cape endemics. One of the ancient lineages included here (Curtisiaceae + Grubbiaceae) is only old enough to be included if combining the mesophytic, plesiomorphic Curtisiaceae with the microphyllous Cape endemic Grubbiaceae; the same would be the case in the marginally more widespread Stilbaceae (not included as it occurs outside Africa) (cf. [22]). It is also interesting that the cycad *Stangeria* occurs in both fire-prone grasslands and fire-free forest environments in SE Africa [23], a plasticity that may have been important in its survival through the ages.

In assessing the potential past movements of the ancient endemic African flora, two aspects need to be considered. On the one hand, unlike birds, where ancient lineages now restricted to Africa (such as ostriches, turacos, mousebirds) were typically more widespread in the Cenozoic [24], there is little evidence that any of the plant lineages listed here previously occurred on other continents [9]. Secondly, the African set of ancient endemic taxa, while inclusive of Madagascar (with numerous shared lineages), was very easy to delimit geographically. Only a couple of lineages are shared with the Arabian Peninsula, and a few (e.g., *Vahlia*, at order level) stretch as far as India, but do not attain a continuum between African-endemic distributions and widespread pan-tropical distributions on the level of the continuum between Africa and Madagascar. These observations are more in line with a younger age (ca. 50–70 Mya—a time when Africa was already isolated from other Gondwanan fragments), as suggested by earlier phylogenies and by the fossil record [9]. However, ages ca. 100 Mya (as indicated in [7]), combined with mostly poor dispersal and localized survival, are not untenable. Further triangulations between the fossil record, phylogeny-derived ages and geographic patterns are likely to narrow down uncertainties in coming years.

A more comprehensive assessment of paleo- and neo-endemism (cf. [2]), along the lines of that performed by Dagallier et al. [8], but including the whole region, could be useful by contrasting the ancient lineages highlighted here against younger ones, and in doing so emphasizing the patterns characteristic to ancient lineages alone. However, there is value in focusing solely on ancient lineages, as done here. It is hoped that the lineages we identified could serve as conservation flagships for the African flora. Further research on their biology and fine-scale distribution could suggest directions towards preserving these most unique African plants in the face of immediate and long-term climate change, as well as other anthropogenic threats.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15091000/s1>, Table S1: The distribution of ancient plant lineages endemic to Africa and/or its islands across ecoregions [13].

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References

1. Forest, F.; Grenyer, R.; Rouget, M.; Davies, T.J.; Cowling, R.M.; Faith, D.P.; Balmford, A.; Manning, J.C.; Procheş, Ş.; van der Bank, M.; et al. Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* **2007**, *445*, 757–760. [CrossRef] [PubMed]
2. Mishler, B.D. Spatial phylogenetics. *J. Biogeogr.* **2023**, *50*, 1454–1463. [CrossRef]
3. Lowenthal, D. Conserving nature and antiquity. In *Man, Nature and Technology*; Baark, E., Svedin, U., Eds.; Palgrave Macmillan: London, UK, 1988; pp. 122–134. [CrossRef]
4. Donoghue, M.J.; Sanderson, M.J. Confluence, synnovation, and depauperons in plant diversification. *New Phytol.* **2015**, *207*, 260–274. [CrossRef] [PubMed]
5. Procheş, Ş.; Ramdhani, S.; Perera, S.J.; Ali, J.R.; Gairola, S. Global hotspots in the present-day distribution of ancient animal and plant lineages. *Sci. Rep.* **2015**, *5*, 15457. [CrossRef] [PubMed]
6. McLoughlin, S. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Aust. J. Bot.* **2001**, *49*, 271–300. [CrossRef]
7. Janssens, S.B.; Couvreur, T.L.; Mertens, A.; Dauby, G.; Dagallier, L.P.; Abeele, S.V.; Vandeloos, F.; Mascarello, M.; Beeckman, H.; Sosef, M.; et al. A large-scale species level dated angiosperm phylogeny for evolutionary and ecological analyses. *Biodivers. Data J.* **2020**, *8*, e39677. [CrossRef] [PubMed]
8. Dagallier, L.P.; Janssens, S.B.; Dauby, G.; Blach-Overgaard, A.; Mackinder, B.A.; Droissart, V.; Svenning, J.C.; Sosef, M.S.; Stévant, T.; Harris, D.J.; et al. Cradles and museums of generic plant diversity across tropical Africa. *New Phytol.* **2019**, *225*, 2196–2213. [CrossRef] [PubMed]
9. Stevens, P.F. Angiosperm Phylogeny Website. Available online: <http://www.mobot.org/MOBOT/research/APweb/> (accessed on 1 March 2023).
10. Liu, Y.; Wang, S.; Li, L.; Yang, T.; Dong, S.; Wei, T.; Wu, S.; Liu, Y.; Gong, Y.; Feng, X.; et al. The *Cycas* genome and the early evolution of seed plants. *Nat. Plants* **2022**, *8*, 389–401. [CrossRef] [PubMed]
11. iNaturalist. Available online: <https://www.inaturalist.org/observations> (accessed on 4 March 2023).
12. Encyclopedia of Life. Available online: <https://eol.org/> (accessed on 3 March 2023).
13. Olson, D.M.; Dinerstein, E.; Wikramanayake, E.D.; Burgess, N.D.; Powell, G.V.; Underwood, E.C.; D’Amico, J.A.; Itoua, I.; Strand, H.E.; Morrison, J.C.; et al. Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience* **2001**, *51*, 933–938. [CrossRef]
14. Environmental Systems Research Institute (ERSI). *ArcGIS*; Version 10.8; Environmental Systems Research Institute: Redlands, CA, USA, 2020.
15. Palazzesi, L.; Gottschling, M.; Barreda, V.; Weigend, M. First Miocene fossils of Vivianiaceae shed new light on phylogeny, divergence times, and historical biogeography of Geraniales. *Biol. J. Linn. Soc.* **2012**, *107*, 67–85. [CrossRef]
16. Barthlott, W.; Lauer, W.; Placke, A. Global distribution of species diversity in vascular plants: Towards a world map of phytodiversity. *Erdkunde* **1996**, *50*, 317–327. [CrossRef]
17. Jansson, R. Global patterns in endemism explained by past climatic change. *Proc. R. Soc. B* **2003**, *270*, 583–590. [PubMed]
18. Pie, M.R.; Caron, F.S. Substantial variation in species ages among vertebrate clades. *bioRxiv* **2023**. [CrossRef]
19. Wickens, G.E. *Ecophysiology of Economic Plants in Arid and Semi-Arid Lands*; Springer: Berlin/Heidelberg, Germany, 1998; ISBN 364-208-089-8.
20. Procheş, Ş.; Cowling, R.M.; Goldblatt, P.; Manning, J.C.; Snijman, D.A. An overview of the Cape geophytes. *Biol. J. Linn. Soc.* **2006**, *87*, 27–43. [CrossRef]
21. Mokany, K.; Jordan, G.J.; Harwood, T.D.; Harrison, P.A.; Keppel, G.; Gilfedder, L.; Carter, O.; Ferrier, S. Past, present and future refugia for Tasmania’s palaeoendemic flora. *J. Biogeogr.* **2017**, *44*, 1537–1546. [CrossRef]
22. Linder, H.P. The radiation of the Cape flora, southern Africa. *Biol. Rev.* **2003**, *78*, 597–638. [CrossRef] [PubMed]

23. Procheş, Ş.; Johnson, S.D. Beetle pollination of the fruit-scented cones of the South African cycad *Stangeria eriopus*. *Am. J. Bot.* **2009**, *96*, 1722–1730. [[CrossRef](#)] [[PubMed](#)]
24. Olson, S.L. The fossil record of birds. In *Avian Biology*; Farner, D.S., King, J.R., Parkes, K.C., Eds.; Academic Press: New York, NY, USA, 1985; pp. 79–238, ISBN 012-249-408-3.

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