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The Greater Midlands—A Mid-Elevation Centre of Floristic Endemism in Summer-Rainfall Eastern South Africa

Clinton Carbutt ^{1,2} ¹ Scientific Services, Ezemvelo KZN Wildlife, Cascades 3202, South Africa² School of Life Sciences, University of KwaZulu-Natal, Scottsville 3209, South Africa; carbutt@ukzn.ac.za

Abstract: The Midlands region of KwaZulu-Natal (KZN) Province in South Africa was hitherto a putative centre of floristic endemism (CFE) based on conjecture. The aim of this study was to empirically explore this concept by delineating unambiguous boundaries for this CFE and documenting the endemic spermatophytes within a conservation framework. The Greater Midlands Centre of Floristic Endemism (GMCFE), a more expanded study area than the parochial Midlands region of KZN, is formally described as southern Africa's 20th CFE. It is a mid-elevation region occupying the greater Midlands of KZN, with extensions of contiguous grasslands extending northwards into southern Mpumalanga and southwards into north-eastern Eastern Cape. This “foothills” CFE covers ca. 77,000 km² of predominantly mesic C₄ grassland, ranging in elevation from ca. 700–2200 m a.s.l. It is congruent with the “sub-escarpment ecoregion,” essentially a composite of the Sub-escarpment Grassland and Savanna Bioregions and the sub-escarpment grasslands of southern Mpumalanga and northern KZN. The GMCFE hosts at least 220 endemic spermatophytes, of which almost a fifth belong to the family Apocynaceae. Families Asteraceae, Asphodelaceae, Fabaceae, and Iridaceae also contribute significantly. Genera *Ceropegia*, *Aloe*, *Dierama*, *Kniphofia*, *Helichrysum*, and *Streptocarpus* contribute the most endemics. More than half are forbs, and almost three-quarters are confined to the Grassland Biome. Endemic radiations are attributed to geodiversity and geological complexity (especially the strong lithological influence of dolerite); physiographic heterogeneity (particularly elevation gradients and variable terrain units); strategic proximity to hyper-diverse temperate and subtropical “border floras”; and localized pollinator-driven adaptive radiations. Of alarming concern is the high number of threatened plant taxa, with ca. 60% of the endemic flora Red Listed in threat categories (CE, E, and VU) or considered “rare”. Extremely low levels of formal protection and poor ecological connectivity, coupled with high levels of land transformation and intensive utilization, render the GMCFE one of the most imperilled CFE in South Africa. Urgent conservation action is required to safeguard this unique and highly threatened “rangeland flora” and stem the biodiversity crisis gripping the region.

Keywords: border floras; conservation profile; C₄ grassland; evolutionary history; foothills; geodiversity; geological complexity; imperilled; spermatophytes; sub-escarpment



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1. Introduction

Our planet supports at least ~346,000 vascular plant species [1], and more are discovered and formally described each year [2]. Scientific debate about the number and possible localities of new and undescribed species—predicted mostly from biodiversity hotspots [3]—adds further intrigue to this rejuvenated age of discovery [3–5], driven largely by the data–technology revolution [6]. Knowledge of how many plants species, where they are located, their potential benefits to mankind, and the relationships between regional floras is paramount to human well-being given the numerous benefits bestowed by the plant world [5,7]. The plant kingdom, as the primary producer, is therefore the “green backbone” for life on Earth.

Global vascular plant diversity is unevenly distributed [8] and assumed to be most concentrated in tropical forest “hotspots” [9]. “Cold spots,” however, also contribute significant plant diversity and should not be overlooked [10]. Southern Africa, and in particular the Republic of South Africa (South Africa), hosts the world’s most species-rich temperate flora [11,12], largely due to the shrubland-dominated, winter-rainfall Greater Cape Floristic Region; the Succulent Karoo; the grassland-dominated eastern Great Escarpment; and its sub-escarpment foothills. Unsurprisingly, 19 centres of floristic endemism (CFE) have been recognized in southern Africa prior to this study [13–16]. CFE are cradles for rapid evolution of new species and museums for relict taxa [17,18], yet their spatial patterns of distribution remain insufficiently understood—a critical impediment to their conservation, management, and sustainable use [19,20].

Are other geographical areas in South Africa worthy of further scrutiny? Such areas may house unique assemblages of plant species found nowhere else in the world. The collective value of myriad range-restricted species may attract greater interest from scientists and practitioners and ultimately increase their long-term persistence. Knowledge gaps of South Africa’s endemic flora contribute to its insufficient protection [21]. Some poorly known regions may potentially hold future economically and medically important species. Not all floristic regions of South Africa are equally studied or adequately known due to geographical and taxonomic sampling biases [21]. Several putative centres await formal recognition. For example, the “Midlands” region was purported a putative CFE for decades, yet never explored further nor substantiated with empirical data beyond conjecture. A “Midlands Centre” was one of six putative CFE identified either within the Grassland Biome or shared between the Grassland and Savanna Biomes [22]. Reference was made to a Midlands region (not centre) in KwaZulu-Natal Province (KZN)—a parochial view encompassing the mid-elevation land between the Drakensberg, Tugela Basin, Zululand, Coast (coastal belt), and Umzimkulu regions of the province [23]. Neither fully satisfy the need to represent a geographically and floristically coherent homologous region hosting a rich endemic assemblage of plant species. Furthermore, the parochial KZN Midlands region is largely synonymous with a single vegetation type, Midlands Mistbelt Grassland. It is the author’s contention that a CFE cannot be defined by only one or two vegetation types.

The aim of this study was to empirically interrogate the putative “Midlands Centre” concept further by (1) delineating the most appropriate geographical boundaries that align meaningfully to a discrete ecoregion encompassing congruent plant distributions; (2) identifying and quantifying the range-restricted spermatophytes endemic to this study region using detailed desktop, field, and herbarium studies; and (3) develop a conservation profile of the study region using Red Listing and other relevant criteria. This study presents southern Africa’s 20th CFE, the Greater Midlands Centre of Floristic Endemism (GMCFE, or GMC), and provides the first profile of floristic endemism for the region. This study concomitantly contributes to a greater understanding of the Grassland Biome and serves as a seminal framework to further explore, analyse, and protect the endemic flora of this region.

2. Materials and Methods

This study combined extensive field, herbarium (institution-based and online-access), and desktop approaches from 2011–2023. Its scope was the spermatophytes (“phanerogams”: Divisions Anthophyta and Cycadophyta). Plant names followed the post-Darwinian, Englerian System of nomenclature [24], and herbarium codes followed the Index Herbariorum [25]. Field work during austral spring and summers (October–early March) was conducted under permits 1785/2008 and OP 69/2019 with landowner permission. Herbarium-based studies were undertaken at the National (PRE, SANBI), Bews (NU, University of KwaZulu-Natal), and Killick (CPF, Ezemvelo KZN Wildlife) Herbaria—the primary herbaria representing the core study area. The author’s specimens relating to this study, including two type specimens and several new records (range extensions), were lodged in NU and PRE. The primary online plant database consulted was the New Plants of Southern Africa (New POSA), the backbone of which is the Botanical Database of Southern Africa

(BODATSA), containing records from PRE, the Compton Herbarium in Cape Town (NBG and SAM), and the KZN Herbarium in Durban (NH) [26]. Threat assessments were based on the Red List of South African Plants Version 2020 of SANBI's Threatened Species Programme [27]. Extinct, taxonomically problematic, and data deficient taxa were included to generate the most comprehensive and accurate conservation profile of endemic plant taxa in the study region. Unfortunately, more recently described species do not currently feature in these databases. Online (digitized) type specimens and other key historical reference collections were accessed via JSTOR Global Plants Database [28], Plants of the World Online Database [29], and the Global Biodiversity Information Facility [30]. Numerous taxonomic accounts in published literature were consulted (Table S1) in concert with regional reference guides by Scott-Shaw [23], Pooley [31], and Boon [32]. Outdated or incomplete published information was supplemented with field knowledge, herbarium studies, and peer review. Reliance on single data sources was avoided where possible. Literature studies harnessed Google® (Mountain View, CA, USA) and Google Scholar® (Mountain View, CA, USA) search engines. Lithology is poorly documented in plant literature and was supplemented by cross referencing georeferenced locality records with a geological map of South Africa [33]. Plant growth forms (functional groups) followed the latest IUCN classification scheme [34], and vegetation types, bioregions, and biome limits followed Mucina and Rutherford [22]. Forest Biome classifications followed Mucina et al. [35]. The endemic total is based on formally described, published species.

The boundaries of the GMC were rigorously delineated. The putative Midlands Centre [22] was spatially too parochial and not fully representative of a discrete ecoregion. However, it formed the basis from which to explore a more geographically coherent and floristically meaningful region. For the sub-escarpment region characterizing the GMC, this had to be a “sub-escarpment ecoregion” aligning floristic and ecological boundaries [36]. Since the GMC is not an escarpment-defined centre, reliance on mapping rugged topography was not always possible. Other composite methods were therefore employed. The study area was informed partly by the Sub-escarpment Grassland and Savanna Bioregions [22]. The lower-western boundary followed the seamless eastern boundary of the neighbouring Drakensberg Mountain Centre (DMC) delineated by Carbutt [15]. The eastern boundary of the GMC was the interface between the Sub-escarpment Savanna Bioregion and the Indian Ocean Coastal Belt Biome. The southern boundary was the juncture between the sub-escarpment and Eastern Cape lowlands, mapped off Google Earth® Pro Version 7.3.6.9345 (Mountain View, CA, USA) following a grid-based, high-resolution method developed by Carbutt [15]. The northern boundary limit was the sub-escarpment catchment of the Vaal River between Carolina and Ermelo, beyond which begin escarpment-based Mpumalanga and Limpopo CFE [13]. The northern boundary incorporated the sub-escarpment grasslands of southern Mpumalanga and northern KZN mapped using Google Earth® imagery as described previously [15].

Recognition of endemic species can be a subjective exercise if not applied consistently within an empirical framework. A simple metric termed the “Endemicity Index” (EI) was developed to objectively select endemic taxa. This index is calculated by subtracting the number of outlying records, each at a quarter-degree grid cell spatial resolution, from 100. A high threshold of 97% endemism was set, meaning that each taxon, to be adjudicated as an endemic, had to have at least 97% of its core range located within the GMC. This equates to allowing for a maximum of three outlying records outside the core endemic range. The EI is the best way to assess and recognize taxa with a clear “Greater Midlands” centre of distribution as the “best fit” summation of a taxon's global pattern of distribution.

3. Results

3.1. Delineating and Defining the Greater Midlands Centre of Floristic Endemism

“Greater” references a wider, more floristically coherent, and ecologically homologous region than the parochial KZN Midlands (Figure 1). The GMC is essentially a mid-elevation, sub-escarpment CFE ranging in elevation from ca. 700–2200 m a.s.l., although most taxa

occur between 1000–1600 m a.s.l. Its terrain morphological classes range from “moderately undulating plains and hills” to “low mountains” [37]. The GMC corresponds largely with the South-eastern Coastal Hinterland Geomorphic Province [38] (Table 1).



Figure 1. Annotated Google Earth® image delineating the Greater Midlands Centre of Floristic Endemism (GMCFE) in eastern South Africa. This CFE is essentially a “sub-escarpment ecoregion” mapped using methods outlined in Carbutt [15]. Abbreviations: KZN, KwaZulu-Natal; LMEE, Limpopo–Mpumalanga–Eswatini Escarpment; NG, Northern Group; CG, Central Group; SG, Southern Group.

Table 1. Summary of the key attributes characterizing the Greater Midlands Centre of Floristic Endemism (GMCFE) in eastern South Africa. Abbreviations: CFR, Cape Floristic Region; DMC, Drakensberg Mountain Centre; EC, Eastern Cape; KZN, KwaZulu-Natal; LMEE, Limpopo–Mpumalanga–Eswatini Escarpment; Mp, Mpumalanga. Terrain units followed Kruger [37] and geomorphic provinces followed Partridge et al. [38]. Broad vegetation types followed Low and Rebelo [39].

Provinces by Contribution (%)	Area (km ²)	Elevation Range (m a.s.l.)	Highest Point (m a.s.l.)	Dominant Eco-Thermal Belts	Geomorphic Province	Terrain Units
KZN (60) EC (23) Mp (17)	77,000	ca. 700–2200 (1000–1600) Mid-elevation Sub-escarpment Foothills	Swartberg Mtn (2322)	Sub-montane Lower-montane	South-eastern Coastal Hinterland	Moderately undulating plains and hills–low mountains

Table 1. Cont.

Rainfall Regime	Rise to Dominance	Dominant Biome	Dominant Bioregion	Dominant Habitat	Dominant Broad Vegetation Types	Dominant Spermatophytes
Mesic Summer (October–April)	Late Oligocene–Early Miocene (34–20 Ma)	Grassland	Sub-escarpment Grassland Bioregion	Moist C ₄ grassland	North-eastern Mountain Grassland; Short Mistbelt Grassland; Moist Upland Grassland; Natal Central Bushveld	Angiosperms
No. of Spermatophyte Taxa	Larger Families	Larger Genera	Floristic Affiliations	Dominant Growth Form	Geodiversity	Geology and Lithology
220 endemics ~3000–4000 flora	Apocynaceae Asteraceae Asphodelaceae Fabaceae Iridaceae	<i>Ceropegia</i> <i>Aloe</i> <i>Dierama</i> <i>Kniphofia</i> <i>Helichrysum</i> <i>Streptocarpus</i>	DMC Afriomontane LMEE Greater CFR Sub-tropical/coastal	Forb	High	Complex; variable; heterogenous
Dominant Lithological Affinity	Threatened or Rare Taxa	Threat Status	Biodiversity Value	Conservation Value	Formal Protection	Connectivity and Ecological Resilience
Dolerite	60%	Highly imperilled (“nature imperilled”)	Globally and regionally outstanding (global centre of plant diversity)	High priority (global biodiversity hotspot)	Extremely low < 1%	Poor; highly transformed or overgrazed

North to south, this CFE stretches from southern Mpumalanga (just north of Ermelo at S 26°18′) through the Amersfoort–Wakkerstroom–Groenvlei complex (“the Enkangala grasslands”) into north-western and northern KZN (as far west as Van Reenen to just beyond Ngome in the east), descending through the KZN Midlands and southern KZN, to Cala in the Eastern Cape at S 31°30′ (Figure 1). Longitudinally, the GMC is bound between E 27°30′ and E 31°30′. Although represented by three provinces, KZN is the epicentre of the GMC both geographically and floristically (Figure 1). The highest point is Swartberg Mtn (2322 m a.s.l.) in southern KZN.

The GMC covers an area of ca. 77,000 km² and is dominated by moist (minimum 500–700 mm MAR) C₄ old-growth grassland in the summer-rainfall region of eastern South Africa (Figure 2; Table 1). This undulating, semi-contiguous grassland is largely congruent with the Sub-escarpment Grassland Bioregion, represented by 18 fine-scale grassland vegetation types and accounting for ca. 21% of the Grassland Biome [22]. The major grassland types are North-eastern Mountain Grassland, Short Mistbelt Grassland and Moist Upland Grassland [39]. A strong rainfall gradient of decreasing rainfall from north-east (ca. 961 mm MAR) to south-west (ca. 423 mm MAR) is prevalent across this bioregion. Regular mists are also a feature of these grasslands, due to the orographic influence of an upland landscape [22]. Less extensive areas of savanna in the Sub-escarpment Savanna Bioregion occur at lower elevations along the GMC’s eastern boundary (Figure 2) and extend inland as “fingers” through drier valleys incised by large west–east flowing river systems (e.g., the Tugela Basin). Major savanna types are Natal Central Bushveld and Coast-Hinterland Bushveld [39]. Furthermore, small patches of afrotemperate Southern Mistbelt Forest (Eastern Cape–KZN), Subtropical Scarp Forest (KZN), and Northern Highveld

Afrotemperate Forest (KZN–Mpumalanga) occur in the GMC [35]. The GMC also includes many palustrine inland wetlands classified as intrazonal Eastern Temperate Freshwater Wetlands [22] or Temperate Grassy and Montane Grassy Wetlands [40].

Foothills approaching the Drakensberg were not included in the DMC [15] and are best accommodated in the GMC [41]. This CFE stretches towards the KZN coastal hinterland in the east. From an eco-thermal vegetation belts perspective, the GMC is mostly sub-montane to lower-montane (low-montane areas off-escarpment and marginal low-escarpment areas immediately beyond the DMC). Although this is a “South African” CFE, a very small proportion of taxa have marginal outliers extending into southern and western Eswatini (accounted for by the EI).

This CFE has three geographical focal areas of sub-regional endemics: Northern, Central, and Southern Groups (Figure 1; Table S1).

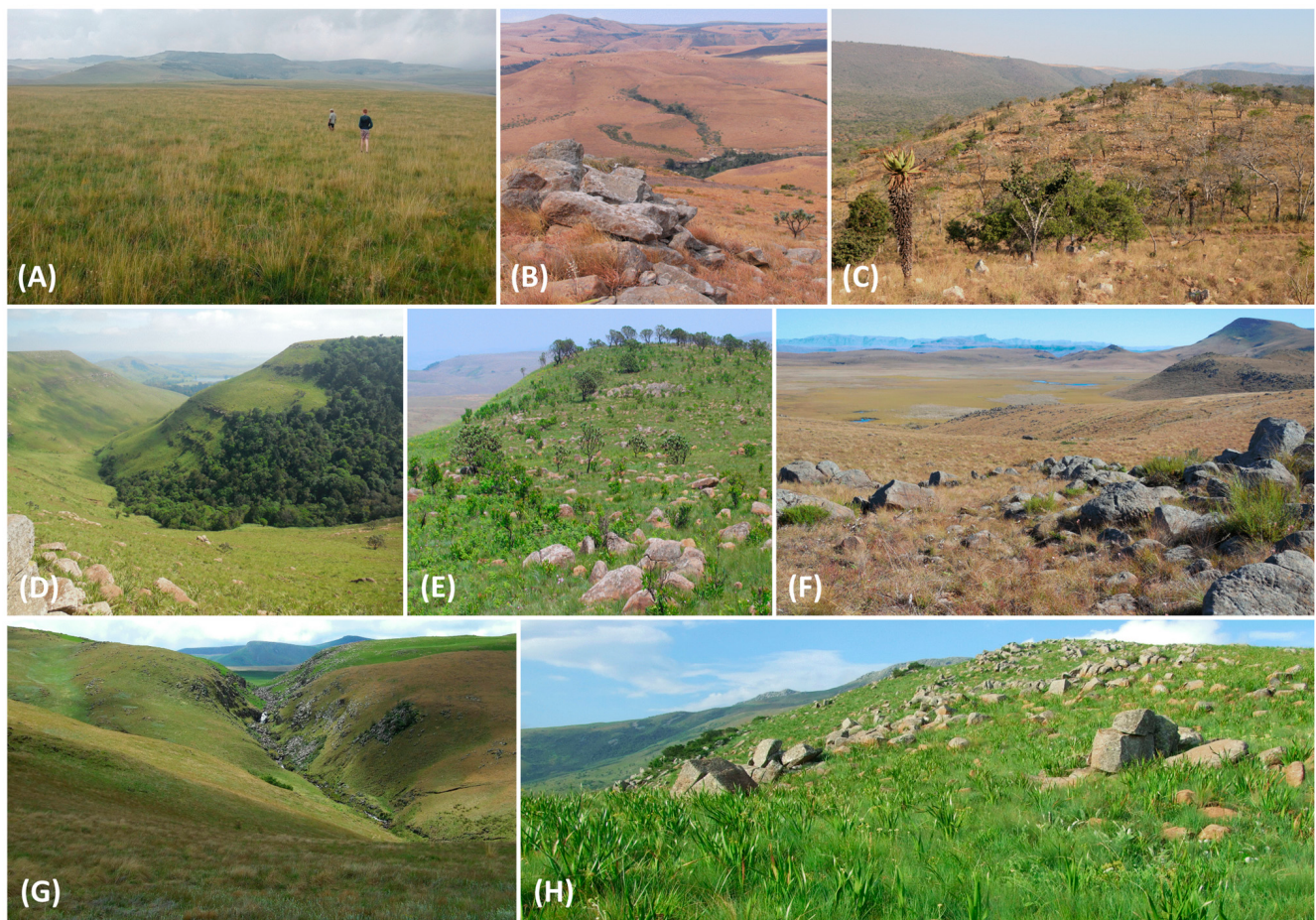


Figure 2. Representative landscapes of the Greater Midlands Centre of Floristic Endemism (GMCFE): (A) degraded, unprotected grassland on dolerite, Groenvlei, northern KZN (Northern Group–GB–early autumn); (B) state protected grassland on dolerite, Ncandu, north-western KZN (Northern Group–GB–late winter); (C) unprotected savanna woodland on quartzitic Mozaan Group sandstone, Louwsburg, northern KZN (Northern Group–SB–late winter); (D) unprotected grassland and Southern Mistbelt Forest on dolerite, Fort Nottingham, KZN Midlands (Central Group–GB–FB–midsummer); (E) privately protected grassland on dolerite, Mt. Gilboa, KZN Midlands (Central Group–GB–late spring); (F) state protected grassland on dolerite, Umgeni Vlei, KZN Midlands (Central Group–GB–late autumn); (G) state protected grassland on dolerite; Ntsikeni, southern KZN (Southern Group–GB–late spring); (H) state protected grassland on dolerite, Mt. Currie, southern KZN (Southern Group–GB–midsummer). All photos by C. Carbutt. Abbreviations: FB, Forest Biome; GB, Grassland Biome; SB, Savanna Biome. Biome limits followed Mucina and Rutherford [22] and Mucina et al. [35].

3.2. Profile of Spermatophyte Endemism

The GMC hosts at least 220 endemic spermatophyte taxa (ca. 98% angiosperms; ca. 2% gymnosperms). More than half belong to the Central Group centred in the KZN Midlands, with smaller percentages associated with the Northern (27%) and Southern (18%) Groups (Figure 3A; Table S1). Endemic taxa are represented by 38 families and 101 genera. Almost a fifth belong to the family Apocynaceae. Families Asteraceae, Asphodelaceae, Fabaceae, and Iridaceae also contribute significantly (18 endemic taxa or more) (Figure 3B). Genera *Ceropegia*, *Aloe*, *Dierama*, *Kniphofia*, *Helichrysum* and *Streptocarpus* account for most endemic species (nine endemic taxa or more) (Figure 3C; Table 1). *Streptocarpus* is the only forest-centred significant contributor of endemics. Several endemic taxa are represented by “Cape element” genera *Disa*, *Erica*, *Gladiolus*, *Hesperantha*, *Holothrix*, *Manulea*, *Moraea*, *Nemesia*, *Osteospermum*, *Phyllis*, *Selago*, *Struthiola*, *Wahlenbergia*, and *Watsonia*. More than half of the endemics are forbs (herbaceous biennials or perennials—hemicryptophytes), followed by geophytes (cryptophytes), shrubs (phanerophytes), subshrubs (chamaephytes), and succulent aloes (Figures 3D and 4). There are very few endemic trees (phanerophytes), vines (lianas or twiners), and only a single endemic graminoid. There are no endemic annuals, hydrophytes, or parasitic plants (Table S1). Almost three-quarters are grassland-dwellers confined to the Grassland Biome (Figure 4), followed by mixed biomes (almost always including the Grassland Biome), while Savanna and Forest Biomes contribute the fewest endemics (Figure 3E). Most endemic taxa are single-biome species, very infrequently multiple-biome inhabitants (mainly grassland–savanna transition areas, e.g., *Aloe inconspicua* Plowes; *Barleria greenii* M.Balkwill & K.Balkwill) or ecotone/forest-edge specialists at the grassland–forest transition (e.g., *Plectranthus rehmannii* Gürke; *Schizoglossum ingomense* N.E.Br.). Just under half of the endemics are restricted to dolerite; followed by dolerite–“other substrates”; sandstone; shale; and gabbro (Figures 3F and 4). Almost 60% of the taxa are Red Listed in threat categories (CE, E, and VU) or are considered rare (Figures 3G and 4). Almost 70% of the taxa are 100% endemic, while 17%, 10%, and 6% have endemism indices of 99%, 98%, and 97%, respectively (Figure 3H).

Certain endemics are eurytopic species spread more widely across the study region (e.g., *Nemesia silvatica* Hilliard; *Pachycarpus natalensis* N.E.Br.), whereas others are highly localized (stenotopic) species (e.g., *Satyrium cernuiflorum* Castañeda-Zárate & van der Niet—pollination ecotype [42]; *Lessertia ingeliensis* M.Balkwill—edaphic specialist). Most species contributors by name are: “*woodii*” (five species), named after pioneering KZN plant collector and curator of the Durban Botanic Gardens, John Medley Wood (1827–1915); “*gerrardii*” (four species), named after English botanical collector, William Tyrer Gerrard (1831–1866); “*natalensis*” (four species), reference to KZN province; and “*tysonii/tysonianum*” (four species), named after South African botanist, William Tyson (1851–1920). The proportion of GMC endemics having DNA sequence data available in GenBank or seeds cyro-preserved in the Millennium Seed Bank is unknown.

3.3. Extra-Limital Species: What Taxa Were Excluded?

Many plant taxa (> 1000) were initially screened. Filtering resulted in ca. 500 candidate species short-listed and subject to further scrutiny. After careful consideration and consistent application of the EI, numerous taxa with other phytogeographic affiliations were excluded. Examples of such taxa are shown in Table S2. DMC near-endemics are covered in more detail in Carbutt [15] and Carbutt and Edwards [43].

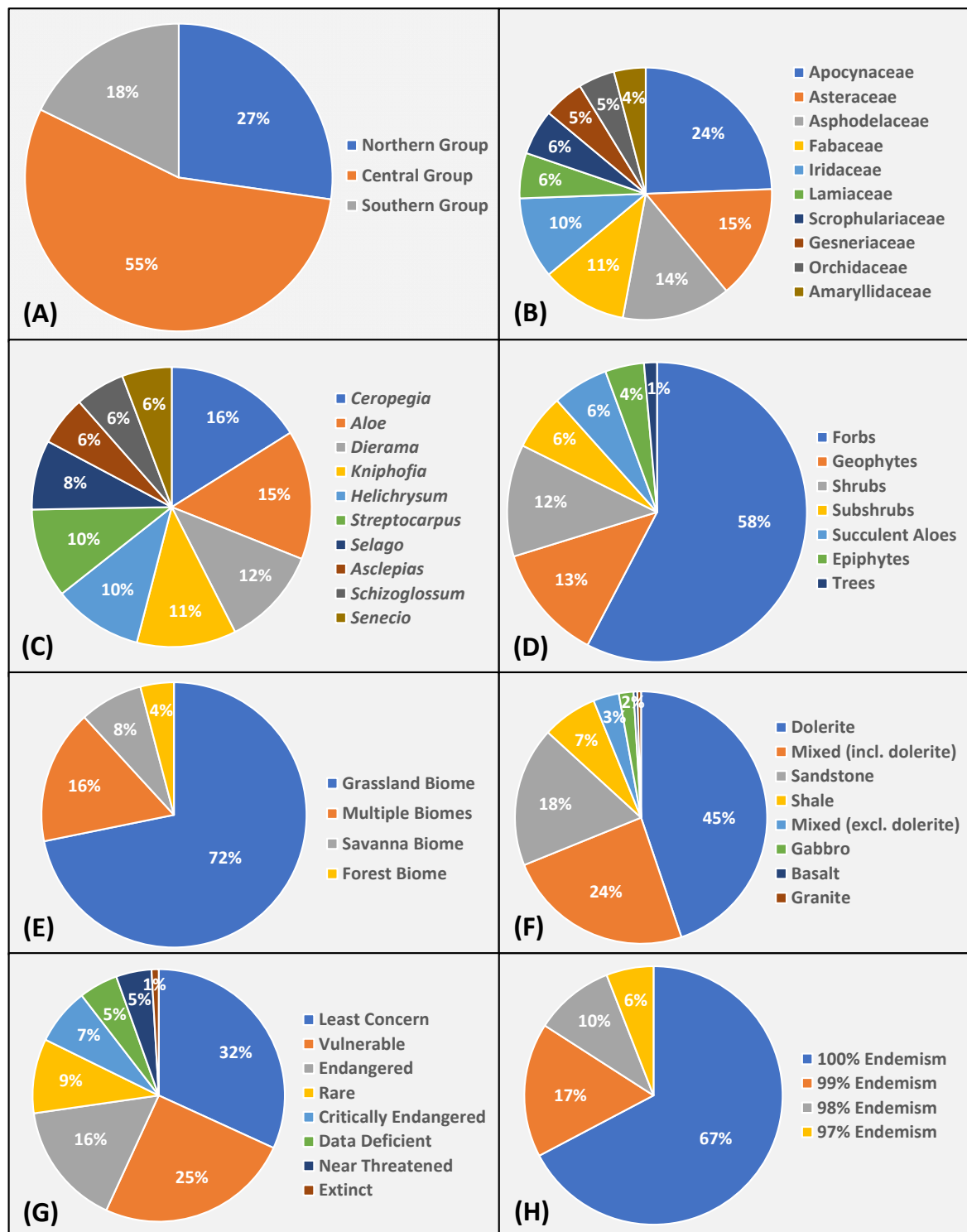


Figure 3. Pie-chart analysis showing the breakdown of Greater Midlands Centre (GMC) endemic spermatophyte taxa arranged by: (A) group; (B) larger families; (C) larger genera; (D) plant growth form; (E) biome; (F) lithology; (G) threat status; and (H) Endemicity Index. All data were arranged from highest to lowest values, except for (A) arranged by northernmost to southernmost latitudes.

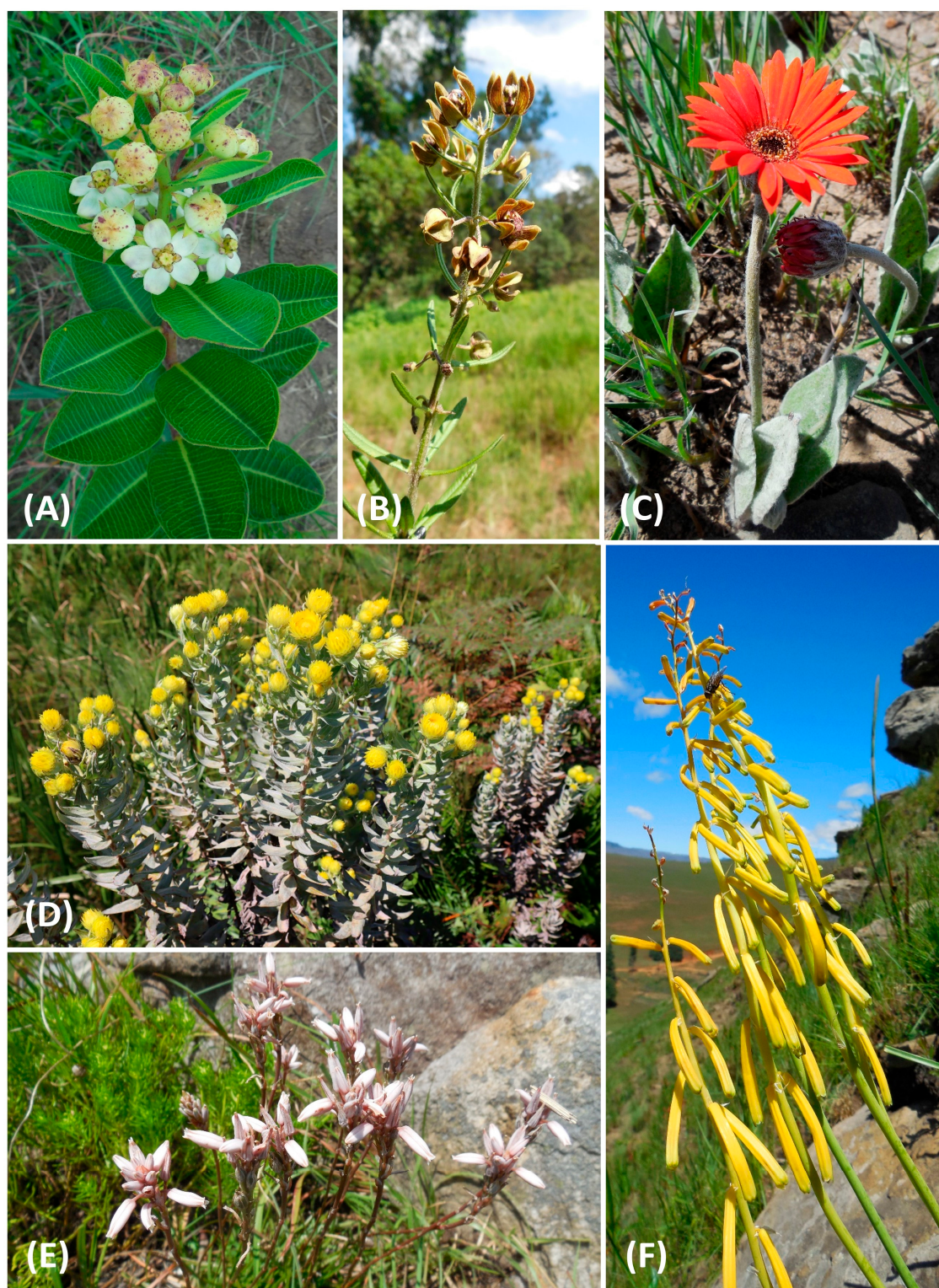


Figure 4. Cont.

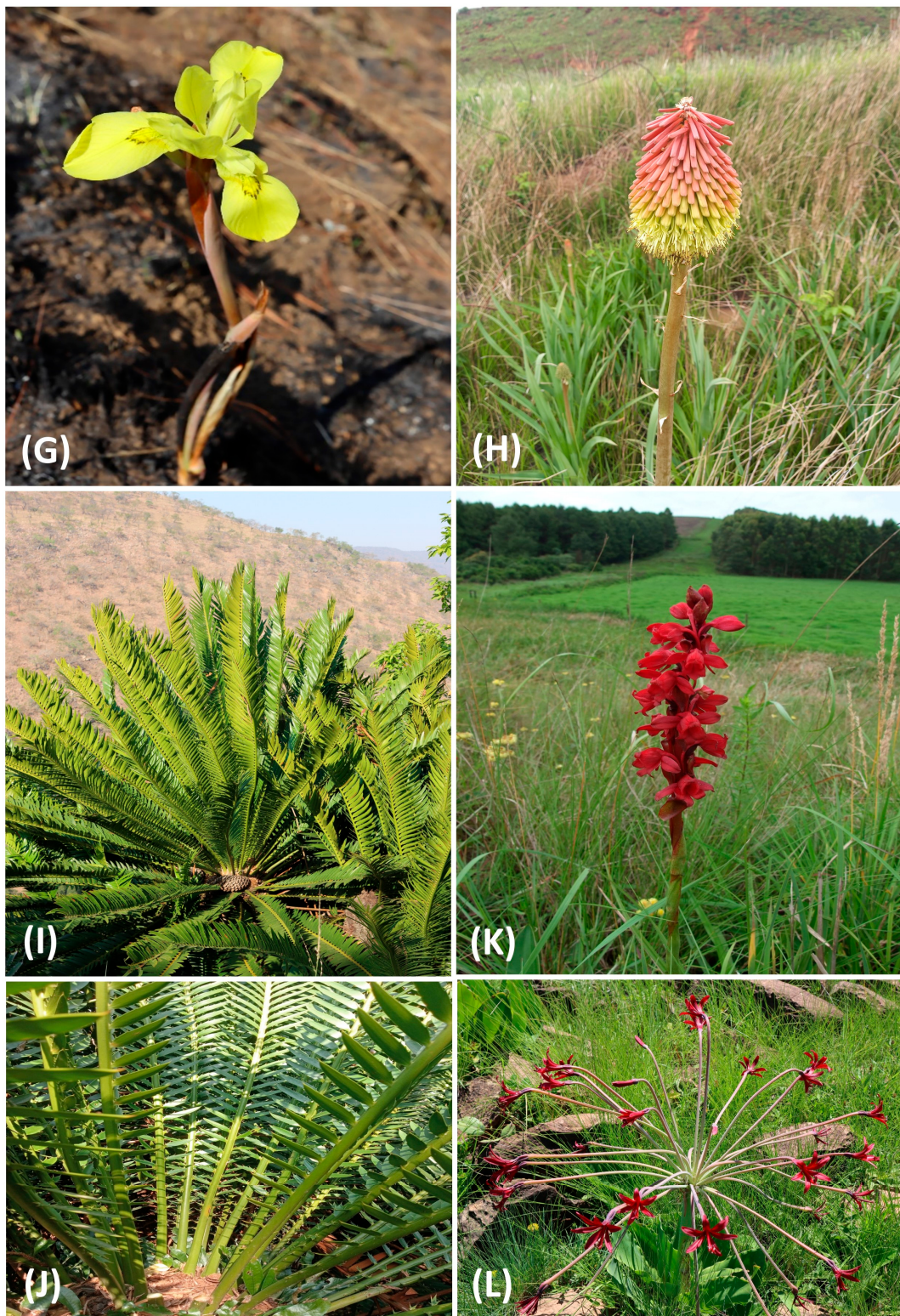


Figure 4. Representative photographic examples of Greater Midlands Centre (GMC) endemic spermatophytes across a range of divisions, larger contributing families, growth forms, and high threat classes: (A) *Pachycarpus acidostelma* M.Glen & Nicholas (Apocynaceae)—CE forb; (B) *Schizoglossum ingomense* N.E.Br. (Apocynaceae)—E forb; (C) *Gerbera aurantiaca* Sch.Bip. (Asteraceae)—E forb; (D) *Helichrysum citricephalum* Hilliard & B.L.Burtt (Asteraceae)—CE shrub; (E) *Aloe saundersiae* (Reynolds)

Reynolds (Asphodelaceae)—E succulent aloe; (F) *Kniphofia ichopensis* Schinz var. *aciformis* Codd (Asphodelaceae)—DD forb; (G) *Moraea hiemalis* Goldblatt (Iridaceae)—VU geophyte; (H) *Kniphofia latifolia* Codd (Asphodelaceae)—E forb; (I,J) *Encephalartos aemulans* Vorster (Zamiaceae)—CE male-coning cycad; (K) *Satyrium rhodanthum* Schltr. (“red form”) (Orchidaceae)—E forb; (L) *Brunsvigia undulata* F.M.Leight. (Amaryllidaceae)—rare geophyte. All photos by C. Carbutt. Abbreviations: CE, Critically Endangered; DD, Data Deficient; E, Endangered; VU, Vulnerable.

4. Discussion

4.1. General Comments

This study presents the first endemic-focused floristic assessment of the GMC and the first sub-escarpment CFE in eastern South Africa. Paucity of mid-elevation CFE in the region prohibits meaningful comparisons with the GMC. The GMC is a geographically discrete area—a key defining criterion for CFE [44]—corresponding essentially to a “sub-escarpment ecoregion,” with marginal sections of low-escarpment along the KZN/Free State border immediately beyond the DMC. Furthermore, it fulfils the requirements of accommodating many range-restricted species with congruent ranges, and it does not intersect with other CFE [15,44]. It also incorporates an area recognized as a putative CFE [22] and aligns phytogeographical and ecological boundaries [36].

The GMC’s 220 endemic taxa is a moderately high total, on par with the neighbouring DMC (227), but the latter occupies half the area [15]. The “area effect” of the GMC’s expansive area dilutes the endemic element, the anchor of a flora, to a small fraction of the total flora (ca. 6–7%), estimated at around 3000–4000 vascular species. Poor gymnosperm representation is partly due to antiquity and association with palaeo-climates [45]. Dominance of angiosperms, globally the largest and youngest phylum of plants, took place during the Cretaceous period (ca. 145–65 Ma) [46,47]. Proliferation of succulent endemics represented by Aizoaceae, Crassulaceae, and Euphorbiaceae, and some Apocynaceae and Asphodelaceae in a mesic summer-rainfall region may be driven by water stress associated with functionally arid habitats such as rocky environments with thin soils. The lower-than-expected number of endemic orchids is probably due to their long-distance dispersal capabilities across open landscapes. The larger families and genera of the GMC mirror those of the Maputaland–Pondoland Region [48]. However, the larger endemic-contributing genera of the GMC, and to a lesser degree families, are not well aligned with those of the DMC [15]. This suggests that the “escarpment” influences of high elevation, rugged topography and orographic climate characterizing the DMC are significant selection forces defining discrete endemic assemblages for certain taxa.

The GMC’s endemic taxa occur predominantly in moist open landscapes characterized by old-growth temperate grasslands assembled over hundreds of thousands of years [49,50]. This is consistent with the neighbouring DMC [15] and Limpopo–Mpumalanga–Eswatini Escarpment (LMEE) [16] as well as the Maputaland–Pondoland Region [48]. This underscores the critical importance of primary grasslands as hyper-diverse storehouses of plant diversity and endemism. The dominance of forbs and poor representation of trees is consistent with a grassland-dominated flora and other regional grassland floras. These grasslands are structured by elevation, frost-driven climate, and vegetation composition—with similar precipitation but warmer temperatures and lower incidences of frost than the Drakensberg Grassland Bioregion [51]. The C₄ grasslands rose to dominance in the late Oligocene–early Miocene (34–20 Ma), a period marked by a depressed CO₂ environment also rapidly cooling, drying, and becoming more flammable [52–55]. Fire is therefore the key disturbance driver maintaining these grasslands [56]. Grasslands of the GMC are characterized by high alpha-, beta-, and gamma-diversity; high compositional turnover results in regionally unique suites of species across the Grassland Biome [57].

The GMC also includes less extensive woody biomes. It is normal for phytochoria to include multiple biomes [13] or elements of other biomes as “biome incursions” [22]. *Streptocarpus*, mostly forest-dwelling, contributes a significant number of endemics despite poor forest representation in the GMC. Larger forests near Ngome, Nkandla, and Qudeni

are important in this regard. The diverse range of terrain units shape this complex endemic landscape and accommodate many critical water catchments and wetland complexes (strategic water source areas)—this high water-yielding ecological infrastructure promotes water security and supports significant regional economies [58].

Pollinator shifts from generalist to specialist syndromes and vice versa may have influenced GMC endemic radiations through pollinator-driven divergence. Apocynaceae, one of the larger angiosperm families globally, is characterized by diverse evolutionary shifts in pollination systems [59]. Endemic radiation of Apocynaceae in the GMC is significant. The “aridity-driven niche divergence hypothesis” links African asclepiad speciation to episodes of climatic cooling and drying [60]. Environmental forces may have also shaped the evolution and diversification of pollination systems in Apocynaceae by mediating pollinator membership through “ecological filtering” [59]. Niche specialization driven by pollination ecotypes has also been documented for the endemic ground orchid *Satyrium cer-nuiflorum* [42]. By contrast, Asteraceae is characterized by shifts from specialist to generalist pollination systems [61].

Herbarium studies (both physical collections and online records) were instrumental in developing an accurate profile of floristic endemism in the GMC. The declining state of plant taxonomic research in South Africa [62,63] and drastic decreases in plant collecting efforts [64] present fundamental challenges to conserving plant biodiversity in South Africa. Since herbaria are the cornerstone of plant taxonomic studies, an appeal is made for herbaria to remain well-resourced and curated. This not only ensures longevity of important historical collections but also preserves critical scientific information not only for plant systematics but also for the evidence-based conservation of South Africa’s rich flora [65]. Herbaria are therefore key to data integrity because they are primary repositories of “raw” data before data are subject to further processing and potential “data corruption”. Data checking and cleaning is critically important in large state-managed databases and herbaria. There are many instances of discord between published taxonomic accounts and SANBI online data, and between the SANBI Red List and New POSA (BRAHMS Online), including many spurious records. Red Lists also require updating; several taxa are more common and widespread than their Red Listing suggests, while the converse also holds true. Newly described taxa are not Red Listed. Elevation data are notoriously absent from historical records.

4.2. Phytogeographical Context and Affiliations

The GMC occurs at the interface of the Sudano-Zambezian and Uzambara-Zululand global floristic regions defined by Takhtajan [66]. It is a regional CFE within the context of southern Africa (in the sense of Van Wyk and Smith [13], not White [67]). It falls within the broader Afromontane and Afroalpine Archipelago-like Centre of Endemism [13,67] at a continental scale. Its broad ties with grassland “islands” of the Afromontane phytochorion [67] occur through taxa represented by *Kniphofia* (Asphodelaceae) [68].

This “missing middle” is surrounded by numerous other CFE: Barberton and Wolkberg Centres [13] to the north or, alternatively, the more generic LMEE “area” of endemism [16]; the Maputaland Centre [13] to the north-east; the Pondoland Centre [13] to the south-east; and the DMC [15] immediately west. High confidence is placed in recognizing the Greater Midlands as a CFE against such a backdrop. It is risky describing a CFE when surrounding areas are not well known botanically, as many of the taxa being recognized as “endemics” may occur in poorly explored surrounding areas (this concern applied to the Sneeuberg Centre, for example, outlined in Carbutt [15]).

Including the Soutpansberg Centre in the extreme north-east, eastern South Africa is now characterized by eight CFE. This attests to remarkable endemic richness in a summer-rainfall landscape. A largely semi-contiguous region of “super-endemism”—accommodating a complex of phytochoria—points towards a nested hierarchy of endemism, which warrants further investigation. There is also a need to test the phylogenetic signal to better understand

the evolutionary history of this sub-escarpment region's endemic taxa in the broader Grassland Phyloregion. This has already been applied to the woody flora of southern Africa [69,70].

Strategically wedged between lowland and high-elevation floras, the GMC is a “tension zone” of multiple phytogeographic influences at a subtropical–temperate interface (Table S2). It is an important “source flora,” contributing genetically to the DMC, the broader escarpment, and the Grassland Biome. Although the GMC is surrounded by other CFE, it shares strongest phytogeographic links at the flora level with the seamless DMC. This applies particularly to the montane “inselbergs” of the GMC. Migrations of taxa from the Midlands region to the DMC may have taken place via corridors such as Ngeli Mtn [71]. The mid-elevation grasslands of the GMC are important sources of phylogenetic lineages for repeated episodes of colonizing the alpine sinks of Africa [72]. Examples include *Helichrysum* (Asteraceae) and *Erica* (Ericaceae) [72,73]. Present-day species distributions may retain some signature of earlier migrations and habitat filtering [70].

The close floristic relationship shared between the Drakensberg and Midlands floras reduces the number of DMC and GMC endemics because numerous taxa have stations in both floras (Table S2; Column 1). Cape element genera are represented as outposts, indicating ties to the Greater Cape Floristic Region, but this representation is not as prolific compared to the DMC and Pondoland Centre [74].

Boundary changes to the Drakensberg Alpine Centre, resulting in the re-defined DMC, have significant permutations for the neighbouring GMC. Formerly, the Drakensberg Alpine Centre included montane outliers located off-escarpment [75]. Alpine and montane areas associated with the escarpment were later represented by a single consolidated boundary, represented as the DMC, which excluded montane outliers now technically occurring in the GMC [15]. This change has two implications: (1) taxa previously recognized as Drakensberg Alpine Centre endemics, occurring exclusively on these montane outliers [43], are not endemic to the DMC but have to be recognized as GMC endemics because they occur only on Greater Midlands inselbergs such as Ngeli Mtn; and (2) taxa previously recognized as Drakensberg Alpine Centre endemics, occurring in the Drakensberg and on these montane outliers [43], are better recognized as DMC near-endemics (Table S2). The GMC is often the only other station for DMC near-endemics and therefore an important “phytogeographic insurance policy” for the DMC.

There is strong evidence of micro-scale endemism, with discrete concentrations of endemics partitioned into three geographical focal areas. It would be premature to regard these areas as sub-centres of endemism without further detailed interrogation. The Northern Group extends from southern Mpumalanga, particularly around Wakkerstroom, across the KZN border to Groenvlei, Luneburg, Utrecht, and Newcastle districts eastwards through Vryheid and Louwsburg to Ngome Mtn (Table S1). The largest concentration of endemics occurs in the Central Group, essentially the KZN Midlands, extending to the foothills of the KZN Drakensberg and eastwards to the coastal hinterland of KZN but may include occasional outliers in northern or southern KZN. The Southern Group covers south-western KZN (e.g., Creighton, Ixopo, Harding, Umzimkulu, and Kokstad districts), including Ngeli, Ntsikeni, Mt. Currie, and Franklin, southwards to the north-eastern Eastern Cape. Each group is separated by a large, more arid, river valley system—the Tugela River Basin separates the Northern and Central Groups; the Umkomazi River Basin separates the Central and Southern Groups. Additionally, several small mountain complexes accommodate steno-endemics such as Ngome Mtn (four species), Ngeli Mtn (four species), and Mt. Gilboa (three species). Large, warm, drier valley systems, such as the Tugela River Basin, also account for localized endemics (nine species), most of which are trees.

There is one geographical area of regional conflict, contending with a small portion of grassland in the northern limits of the GMC previously included in the LMEE. This area is better placed in the GMC because (1) the sub-escarpment defined GMC (incorporating the Sub-escarpment Grassland and Savanna Bioregions) should also include the contiguous sub-escarpment grasslands of southern Mpumalanga and northern KZN; (2) the LMEE is described as an “escarpment-based” area of endemism; (3) the southernmost CFE in

Mpumalanga and Limpopo, namely the Barberton and Wolkberg Centres [13,76], extend as far south as Barberton–Carolina; they also exclude the southern Mpumalanga grasslands; (4) geologically, Carolina marks the approximate end of both Karoo Supergroup dominance and the strong influence of dolerite, giving way to the Barberton and Transvaal Supergroups under strong serpentine and dolomitic influences, respectively; (5) the forest biome classification shows Northern Mistbelt Forest beginning near Barberton [35], providing further evidence of key floristic shifts in this region; and (6) further evidence is found in the distribution of classic “Midlands” plant endemics. For example, the iconic Hilton Daisy (*Gerbera aurantiaca* Sch.Bip.), although centred in the KZN Midlands, extends into southern Mpumalanga (see Carbutt 20 of 2017 NU; Table S1), demonstrating a floristic association between these contiguous grassland regions. A host of other endemic plant taxa bear witness to this pattern (Table S1, Northern Group). Intuitively and evidence-based, the southern Mpumalanga and northern KZN grasslands, unassigned to any previously recognized CFE, are best accommodated in the GMC. The LMEE “area” of endemism, not defined as a CFE [16], is therefore difficult to place in the regional endemism landscape, especially given that three discrete and edaphically nuanced CFE have been documented in this region. The LMEE is generous for an “escarpment-based” region and does not exclusively represent a geographically discrete region—a key prerequisite for defining CFE [44]. The sub-escarpment areas of the “escarpment based” LMEE are better placed in a sub-escarpment CFE, where regional, phytogeographical, and ecological boundaries align [36].

4.3. Role of Geological and Lithological Drivers

Centres of vascular plant diversity and endemism are characterized by high geodiversity—the diversity of the abiotic environment [8,19,61,77]. Geologies and weathering patterns influence soil formation and thereby the membership of plant communities [78,79]. Geological heterogeneity increases habitat diversity by facilitating specializations to a wider variety of soil types as they are exposed or created by erosion; it also results in a more complex landscape due to differences in erodibility [80]. The GMC occupies the South-eastern Coastal Hinterland Geomorphic Province, an area of considerable geological diversity [38] further characterized by a complex arrangement of highly variable terrain classes [37].

The Northern Group is associated with the Kaapvaal Craton (3 Ga), an ancient crustal block accounting for the northern limits of the GMC. The Central Group begins approximately at the Tugela Fault (Tugela Thrust Front), where the Kaapvaal Craton gives way to another archaic foundation, the Natal Metamorphic Province (1 Ga). This Province also accounts for the Southern Group. Superimposed on this basic template are a range of geological deposits and intrusions in the GMC. Kaapvaal Craton basement granite, and Pongola granite, Mozaan Group sandstone and shale, and Nsuze Group basalt and sandstone (of the Pongola Supergroup) (3–2.8 Ga) [81] occupy the GMC’s north-eastern limits. Its eastern margin is characterized by localized sandstone exposures of the Natal Group (490 Ma). The remainder of the GMC, accounting for its largest area geologically, is associated with the Karoo Supergroup (Dwyka, Eccca, Beaufort, Stormberg, and Drakensberg Groups) [38]. Overlying the Natal Group is a thick unit of Dwyka Group tillite (300 Ma) deposited in a glacial environment by retreating ice sheets [33,82]. This tillite extends north to south in a thin band through the central GMC. Outcrops of the Eccca Group (280 Ma)—shales of the Pietermaritzburg Formation, sandstone sediments of the Vryheid Formation, and siltstones of the Volksrust Formation—extend throughout its northern, central, and southern parts. Mudstone and sandstone sediments of the Beaufort Group (250 Ma) dominate the GMC’s western boundary (except in the south-west) and form the foothills leading up to the Drakensberg escarpment [33,82]. Sediments of the Stormberg Series (240–190 Ma) marginally occur in the south-western limits of the GMC. Pockets of Drakensberg Group dolerite (190–180 Ma) extend throughout the north-western, western, southern, and central parts of the GMC. Dolerite sills are scattered throughout inland KZN in sedimentary rocks of the Karoo supergroup [33,82]. Several doleritic and gabbroic

intrusive sheets such as the Insizwa–Ngeli–Tonti–Tabankulu complex, 175 km southwest of Durban, span southern KZN and north-eastern Eastern Cape [83–85].

Radiation of the endemic (and presumably the total) flora of the GMC is linked, in part, to the complex geological heterogeneity of the region. Strong associations with single geological types are testament to narrow edaphic affinities. Intrusive dolerite exerts a strong influence over almost 70% of GMC endemics, accounting for key endemic strongholds at Balelesberg (Utrecht), Ngome, Mt. Gilboa, Ntsikeni, and part of Ngeli Mtn. Dolerite is largely overlooked as a lithological driver of plant endemism. The strong association between GMC endemics and dolerite is disproportionate to its extent, relegated to scattered “edaphic islands” within a far more heterogeneous geological matrix. Interestingly, dolerite is the youngest geological type in the GMC. This suggests that the significantly large cohort of dolerite-dependent endemic taxa may be holo-endemics (habitat specialists) or possibly neo-endemics (evolutionary younger taxa). Daru et al. [70] determined that the flora and vegetation of southern Africa is relatively recent (40–20 Ma). However, CFE can contain neo- and palaeo-endemics—“centres of mixed-endemism” [20]—and this scenario likely applies to the Grassland Phyloregion [70] and GMC. Far fewer endemics are linked to skeletal sandstones of the Natal Group and sandstone deposits of the Karoo and Pongola Supergroups. Smaller contributions are made by shale, gabbro (Ngeli Mtn and Mt. Insizwa), basalt, and granite.

The GMC and DMC are heavily associated with igneous-affiliated substrates of the Drakensberg Group (dolerite and basalt respectively), possibly influencing their close floristic relationship through rock and soil chemistry. Igneous-based substrates are also known to be associated with high alpha-diversity in the Grassland Biome [57].

4.4. Conservation Imperatives

The GMC occurs almost exclusively within the Maputaland–Pondoland Region, one of 20 global centres of vascular plant diversity [8]. It also occurs within the Maputaland–Pondoland–Albany Biodiversity Hotspot, the second richest floristic region in Africa after the Greater Cape Floristic Region [86] but remains a biodiversity knowledge gap [21]. Biodiversity hotspots, by definition, have experienced a significant degree of transformation within an endemic-rich landscape [87]. This context illustrates the global significance of the GMC. South Africa’s biodiversity hotspots carry high extinction risk [88,89] because most ecosystems in South Africa have been modified or transformed by human activity [21,23,90]. South Africa is therefore an Important Plant Area (IPA), a globally important site for threatened plants and their habitats in a botanically rich area [91,92]. IPAs provide a framework for implementing Target 5 of the CBD Global Strategy for Plant Conservation to ensure protection of at least 75% of an IPA [92]. Recently acquired knowledge of new CFE such as the GMC should adaptively inform reviews of global plant conservation strategies [93].

Almost 60% of the GMC endemic flora is threatened with extinction, more than four times the national (14%) [94] and three times the global figure (20%), respectively [95]. Forbs (hemicryptophytes), the dominant functional group of GMC endemics, are the most prone to extinction [89]. Most of the CE endemics are cycads or asclepiads. Cycads (Cycadales–Zamiaceae) are one of Africa’s ancient phylogenetic endemic lineages likely older than 100 Ma [45] and amongst the most threatened plant groups on Earth with 60% at risk of extinction [96]. This is attributed to high levels of illicit harvesting for the horticultural trade (private collections and landscaped gardens) and traditional medicine [97,98]. Ancient floristic lineages such as cycads are high conservation priorities [45]. Several CE Apocynaceae are highly range-restricted, known only from single localities, rendering them extremely vulnerable to extinction. Conservation initiatives should also not lose sight of LC taxa given the current pressures facing plant species and high rates of land conversion and intensification. Ironically, endemics often hardest to detect are not those in high threat categories as they are usually well known for their “rarity” and feature prominently in Red

Data accounts. Rather, taxa more widespread throughout their endemic range often remain undetected and are highly susceptible to the “tragedy of the commons” principle.

The GMC’s grasslands are most at risk; numerous grassland vegetation types are listed threatened terrestrial ecosystems (South African Government Gazette 47526, Notice No. 2747). They are predisposed to transformation, degradation, and intensive use [7]. This is driven largely by agroforestry, open-cut coal mining, agriculture, urban expansion, overgrazing, invasive alien plants, illegal plant harvesting, and insidious rural sprawl [50]. Since long-term climatic stability is an important contributor to accumulating endemic species [18], climate change is a growing concern with potentially catastrophic implications [19]. Grasslands characterized by high species richness and turnover, such as those of the GMC, are therefore more predisposed to losses of unique suites of restricted species, even at small spatial scales of anthropogenic transformation [57]. Native temperate grasslands are the most poorly protected terrestrial biome globally—only 5.5% are formally conserved [7]. The temperate Grassland Biome accounting for most of the GMC is particularly imperilled, with only ca. 2% formally protected [50,99]. The Sub-escarpment Grassland Bioregion, with which the GMC is heavily aligned, is the most poorly conserved of the Grassland Biome’s bioregions—only ca. 1% is formally protected [99]. This falls considerably short of the Aichi Target 11 of 17% protection for all terrestrial ecosystems by 2020 [100] and the highly ambitious revised post-2020 Target 3 of 30% of all land areas conserved in an ecologically representative system of protected areas by 2030 [101].

The GMC is therefore one of South Africa’s most poorly conserved and highly threatened CFE. A high proportion of GMC endemics do not occur in protected areas partly because these formal conservation areas are relatively few and mostly small- to medium-sized (<10,000 ha). Examples include Paardeplaats (southern Mpumalanga), Vryheid Mountain, Ngome, Chelmsford, Ncandu, Blinkwater, Fort Nottingham, Impendle, Karkloof, Midmar–Thurlow, Mt. Gilboa, Vemvaan (Wahroonga), Nkandla, Ntsikeni, Spioenkop, Umgeni Vlei, Wagendrift Dam and Moor Park, Weenen, Mt. Currie, and Constantia (all KZN). The largest protected area in the GMC is Ithala Game Reserve in northern KZN (ca. 30,000 ha). The GMC in southern Mpumalanga and north-eastern Eastern Cape is largely unprotected. These protected areas are experiencing unprecedented community pressure and a surge in unlawful extractive natural resource use, no longer subsistence based. Their value, both individually and collectively, is highly disproportionate to their relatively small size and cannot be overstated. Conservation management authorities should better understand the context in which these protected areas function—they occur within a CFE and a globally important centre of plant diversity hosting irreplaceable phylo-diversity and distinctive evolutionary history. Unfortunately, these smaller protected areas are experiencing attrition in funding and capacity [102], when pressures are increasing and more land is required to secure a highly imperilled CFE.

The GMC is characterized by a “rangeland flora” in a highly fragmented and heavily utilized working landscape [50,58], most of which is under private or communal ownership. Its degraded landscapes have high livestock numbers, low ecological resilience, and poor connectivity. Moderate to high domestic ungulate grazing pressure in high biodiversity mesic grasslands in South Africa depletes forb species diversity [103], rendering plant biodiversity in the GMC highly vulnerable to overgrazing. The GMC lends itself to protection through the Biodiversity Stewardship Programme facilitated by state–conservation NGO partnerships to gazette privately protected lands [58]. Additionally, numerous initiatives have been designed to mainstream biodiversity conservation in production sectors through the SANBI Grasslands Programme [58].

5. Conclusions

New CFE are exciting frontiers of botanical exploration. Presented here was the first in-depth assessment of the imperilled endemic flora of the GMC. It serves as a seminal framework to interrogate specific aspects of the CFE in more detail, such as GIS-based analyses relating to vegetation types, geology, and protected areas, as well as multivariate

explorative analyses such as a cluster analysis. Comparisons with measures of phylogenetic diversity and endemism also need to be made.

Old-growth mesic grasslands (and shrublands) of the summer-rainfall region in eastern South Africa (and parts of Lesotho and Eswatini) occupy numerous CFE. These open ecosystems dominate moderate to high elevations, and their contribution to regional diversity and endemism is underappreciated by local and global northern hemisphere communities. They could perhaps form centres of “super-endemism,” a testament to the remarkable botanical wealth of global significance in the region, but this requires further testing using robust phylogenetic approaches. Their evolutionary, ecological, and ethnobotanical value have not been fully comprehended, and the low levels of protection are a sobering reminder to the custodians that have been entrusted with their conservation. Endemic radiation within the Apocynaceae is noteworthy. The influence of geo-edaphics, particularly dolerite, has not been sufficiently appreciated as a significant driver of endemism in the GMC or South Africa.

The GMC remains a relatively poorly known floristic entity, particularly in its northern and southern recesses. No doubt many new species will come to the fore in this rejuvenated age of discovery and increase the endemic total further. The Greater Midlands is not only a CFE but also an important contributor to regional plant diversity.

Significant conservation interventions are required to stem the loss of endemic species and their evolutionary history. The protection of critical habitats is essential to arresting the biodiversity crisis gripping the region. Given their perilous future on rapidly transforming lands, these endemic taxa should become a priority for DNA sequencing in GenBank and seed cyro-preservation in the Millennium Seed Bank repository. Finally, ex situ conservation measures growing representative GMC endemics in botanic gardens should also be employed as an insurance policy in the face of extirpations.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15111137/s1>, Table S1: Summary of the spermatophytes endemic to the Greater Midlands Centre of Floristic Endemism; Table S2: Examples of extra-limital plant taxa not recognized as GMC endemics; References [104–217] are cited in the supplementary materials.

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