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Madagascan highlands: originally woodland and forest containing endemic grasses, not grazing-adapted grassland

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Long considered a consequence of anthropogenic agropastoralism, the origin of Madagascar's central highland grassland is hotly disputed. Arguments that ancient endemic grasses formed grassland maintained by extinct grazers and fire have been persuasive. Consequent calls to repeal fire-suppression legislation, burn protected areas, and accept pastoralism as the 'salvation' of endemic grasses mount, even as the International Union for Conservation of Nature (IUCN) declares 98% of lemurs face extinction through fire-driven deforestation. By analysing grass data from contemporary studies, and assessing endemic vertebrate habitat and feeding guilds, we find that although the grassland potentially dates from the Miocene, it is inhospitable to endemic vertebrates and lacks obligate grazers. Endemic grasses are absent from dominant grassland assemblages, yet not from woodland and forest assemblages. There is compelling evidence that humans entered a highland dominated by woodland and forest, and burned it; by 1000 current era (CE), grass pollens eclipsed tree pollens, reminiscent of prevailing fire-induced transformation of African miombo woodland to grassland. Endemic grasses are survivors from vanished woody habitats where grassy patches were likely small and ephemeral, precluding adaptive radiation by endemic vertebrates to form grazing-guilds. Today forests, relic tapia woodland, and outcompeted endemic grasses progressively retreat in a burning grassland dominated by non-endemic, grazing-adapted grasses and cattle.

1. Background

Anthropogenic deforestation of islands has happened throughout history. Madagascar's burnt and grazed central highland grassland, from which woodland-dependent megafauna has been lost, has long been considered a degraded forest system [1–3]. Countrywide loss of half the remaining forests in just three decades, and progressive expansion of grassland has bolstered this perspective [4,5]. In 2008, Bond [6] challenged this view. The challenge has gained support from studies on endemic grasses dating from the Miocene [7,8], thought to form naturally extensive grassland adapted to pre-human fire and ostensibly to giant tortoise and hippo grazing-guilds [9,10], with a 5% woodland cover limited naturally by rainfall and climate [9]. This view reflects present circumstances: 70% of Madagascar is grassland, and a small fraction of highland grassland remains wooded [9]. Cattle have been recently proposed as a 'megafaunal substitute facilitating... persistence of a grazer-maintained grass assemblage' ([10], pg. 1), replacing extinct grazers, which along with intensive anthropogenic fires sustain grassland ecological processes and protect endemic grasses.

In stark contrast with these conclusions, the IUCN reports that 103 of 107 lemur species face extinction from slash-and-burn deforestation [11]. In this context, calls to recognize Madagascar's highland as natural subtropical grassland, reverse fire-suppression legislation, start burning conservation areas [12], and adopt pastoralism and anthropogenic fires as suitable proxies for maintaining

natural processes [10,12] will be devastating to biodiversity, if incorrect. Many studies suggest this view may indeed be erroneous: evolutionary [4], archaeological [13], ecological [5], palaeoecological [2], and cultural data [14] provide convincing evidence that these grasslands are anthropogenic (e.g. pollen records signify rapid transformation from trees to grassland, and charcoal particles substantiate the burning of woodland, within the last millennium [2]). Also incongruous is that a grass-covered island should harbour a fauna in which more than 90% of species are forest-adapted [5]. A series of studies by many of the same authors arguing for ancient herbivore-controlled grasslands contradict that conclusion. For example, in 2016 Vorontsova *et al.* [7] found that grazing significantly impacts endemic grasses and grasslands, which they suggest evolved with little or no grazing. This is at odds with the 2020 conclusion of Solofondranohatra *et al.* ([10], p. 1) that ‘grazer-dependant grasses can only have coevolved with a now-extinct mega-fauna’. Although Solofondranohatra *et al.* ([10], p. 2) go on to acknowledge ‘evidence to support a grazer assemblage is limited’, the latest Edinburgh Royal Botanic Garden 2020 press release pertaining to Madagascan highlands is entitled ‘Grasslands: Not Wastelands But Creations of Ancient Creatures’ [15].

Over 95% of Madagascan highland (750 m–1800 m above sea level) grassland is treeless, with the remainder being two distinct woody habitats. These take the form of either open-canopy *Uapaca* woodland (dominated by *Uapaca bojeri*, with or without a herbaceous understorey; and which may be relics of an extensive open-canopy woodland formation, or of a more closed-canopied forest-like system with only fire-resistant *U. bojeri* persisting following the fire-induced loss of a more complex canopy), or closed-canopy subhumid forest in varying states of degradation [4,10]. Adaptive radiation facilitates faunal speciation at the interface of contrasting ecological niches [16]. Thus, an ancient and expansive grassland subjected to natural fire and grazing would be expected to have evolved endemic, species-rich grass assemblages adapted to the disturbance regime [10]. Furthermore, palaeoecological evidence should affirm paucity of tree cover, absence of forest-adapted vertebrates, and a subfossil grazing-guild [10]. If, however, human arrival is coeval with accelerated loss of woodland (and associated folivores), then regional endemic grasses as remnants of woodland-adapted guilds, naïve to grazing and frequent fire, would be absent from dominant guilds, species-poor, and competitively excluded from a system favouring disturbance-adapted forms [7].

The question of an extensive central highland grassland pre-dating human impacts, undergoing top-down control through fire and grazing, with climatic limitations to woody cover [6,7,9,10] is complex. Large, ancient, grazed, fire-dependent grasslands will have; (a) fauna dominated by grassland-adapted taxa, (b) evidence of an obligate grazing-guild, (c) palaeoecological confirmation of grassland, and (d) endemic grasses well adapted to fire and grazing. Having made the case for an ancient grazing-guild, Solofondranohatra *et al.* ([10], pg. 2) emphasize that the interpretation of ‘the links between grasslands and the extinct fauna is crucial to determining the pre-settlement extent of the C₄-dominated grassy biomes’. To assess this, we ask:

- (a) What proportion of Madagascan endemic vertebrate taxa are grassland adapted and is this similar to Australia, the

only other isolated East Gondwana tropical grassland system?

- (b) How well are grazing species represented within central highland subfossil Madagascan herbivore assemblages that existed when humans arrived, relative to other East Gondwana subtropical grassland systems?
- (c) What does the palaeoecological record suggest was the predominant highland ecosystem when humans arrived?
- (d) Do data from recent studies reflect the adaptation of endemic grasses to grazing and intensive fire regimes?

2. Materials and methods

(a) Vertebrate taxa adapted to grassland

Using the ‘Habitat and ecology in detail’ data field from IUCN species assessments, we compiled a database pairing 839 taxa with habitat (forest or grassland adaptation, electronic supplementary material, S1). We included every endemic Madagascan mammal radiating from a single colonization event (i.e. lemurs, euplerids, tenrecs, and rodents), and all reptiles and birds. We did the same for Australian endemic mammals. We then compared the number of species in these groups adapted to either grassland, forest, or either habitat, between the two countries, designating species as either ‘grassland’ (grassland-limited) or ‘not’ (forest or either habitat), using a Wilcoxon rank sum test with continuity correction. Regional endemics (co-occurring on the Mascarenes, Tasmania, and New Guinea) were excluded, as were predominantly aquatic birds, reptiles, and monotremes, groups neither forest nor grassland adapted.

(b) Comparing Madagascan and East Gondwanan herbivore guilds

Given Africa separated from East Gondwana 155 Mya, India from Australia 130 Mya, and Madagascar from India 88 Mya, we compiled a database for the three established East Gondwana tropical grasslands: Australia, East Africa, and the Indian Terai-Duar, and compared herbivore guilds with a Madagascan suite comprising the only extant large herbivore (*Lemur catta*), and subfossils present in the highlands when humans arrived (25 species, *ca* 2500 bp [4]; electronic supplementary material, S2). Guilds were divided into predominant browsers and folivores, obligate grazers and mixed-feeders, informed by a literature review of subfossil isotopic $\delta^{13}\text{C}$ content [1,17], which differentiates C₄ grass diets from C₃ woody diets. To assess for an obligate Madagascan grazer-guild, we compared grazers to non-grazers across guilds and regions using a χ^2 test, with Fisher’s exact test.

(c) Highland palaeoecological record

We tabulated data from an extensive body of research on tree and grass pollen, charcoal deposits (signifying burning of woodland), dung *Sporormiella* fungal spores (proxies for megafaunal biomass [18]), isotope-dated subfossils, human activities, and climate.

(d) Relative representation of endemic grass species under fire and grazing

We assessed and interpreted results from contemporary studies [7,9] to highlight the percentage of narrow endemic grass species in the highland relative to other ecoregions, and evaluated the proportion of endemic grasses in dominant suites across highland vegetation types (electronic supplementary material, S3a,b). Next, using grasses from a fire-adapted functional group established by Solofondranohatra *et al.* [10], we compared number of

Figure 1. Percentage of endemic Madagascan vertebrate groups, Australian diprotodonts, polyprotodonts, and endemic rodents, adapted to predominantly forest, grassland or to both habitats. (Online version in colour.)

sites occupied by endemic and non-endemic grasses to assess relative representation of endemics among dominant assemblages (electronic supplementary material, S3c). Lastly, we analysed data from 16 highland sites collected in December 2013 by Vorontsova *et al.* [7] to assess the impact of fire, grazing, and altitude on the proportion of endemic grass species within sites. Grazing and fire represent the prevailing highland disturbance, impacting grasses in tandem, so we combined these two components to establish a variable that encapsulates the disturbance regime, by adding grazing (presence/absence) as recorded by Vorontsova *et al.* [7] and the frequency of fire over the three years preceding the data collection (2011–2013), using NASA Moderate Resolution Imaging Spectroradiometer data [19] (electronic supplementary material, S3d). If endemic grasses evolved in an ecosystem influenced by fire and grazing, they should be tolerant of these disturbances, and well-represented relative to non-endemics. We used a generalized linear model with the number of endemic grass species versus non-endemics per site as the response variable, and altitude and disturbance regime (i.e. grazing index + fire frequency) as explanatory variables, binomial family with probit link. We validated the model by visual inspection of residual plots, Q-Q plots, and Cook's distance [20].

3. Results and discussion

(a) Vertebrate taxa adapted to grassland

Distinct biomes facilitate speciation. Madagascar comprises four distinct biomes, central highland grassland, eastern rainforests, southern arid spiny forest, and western deciduous forest [4]. Given a single radiation event from Africa for each of lemurs (50 Mya), tenrecs (35 Mya), euplerids (20 Mya), and Nesomyinae rodents (20 Mya), evolutionary adaptation to vast and ancient grasslands that date to the Miocene would be expected if grasslands were indeed an ancient and dominant habitat [16,21]. Yet all euplerids and 98% of lemurs are forest-limited; no tenrecs, only 4% of rodents, 2% of reptiles, and 3% of birds are

grassland-limited (figure 1). All birds with ancient phylogenies have radiated into species-rich, forest-limited families (e.g. Brachypteraciidae, Philepittidae, Mesitornithidae, Vangidae). No lemurs, tenrecs, or euplerids are obligate grassland specialists.

The island-continent Australia provides a temporal and spatial evolutionary parallel: Australidelphia radiated some 70 Mya into Diprotodontia and Polyprotodontia [22], and Miocene and early Pliocene speciation generated Dasyurini, Phascogalini, Sminthopsini (*ca* 12 Mya), and later Planigalini (6.5 Mya). Australian endemic rodents have been radiating since the close of the Miocene 5 Mya [16]. Australian groups are evenly adapted to the different habitats, well-represented in grassland, and significantly different in habitat representation to Madagascar, where proportion of grassland-limited vertebrates approaches zero ($W = 18$; $p = 0.027$; median for Madagascar = 2.5, s.e. = 1.28; median for Australia = 16, s.e. = 3.93; electronic supplementary material, S4a).

Were a single vertebrate group to fail to adapt to a niche that comprises three-quarters of available habitat, that would be an improbable outcome. Yet on Madagascar, all six groups evaluated are excluded from the largest available ecosystem (covering 70% of the island). This either exposes an evolutionary anomaly, or is evidence that extensive grasslands are new. Adaptive change requires time and persistence of habit; conversely, rapid habitat change can cause extirpation of organisms not suited to the transformed environment. Coincident with grass pollens replacing highland tree pollens only 10 centuries ago [2], nine forest-adapted extant lemur species, and an extinct megafauna encompassing hippos, giant tortoises, elephant birds, and giant lemurs disappeared from the highlands and were predominant C_3 woody plant feeders, or mixed-feeders [4,23]. The evolutionary inconsistency presented by all single-lineage Madagascan endemic vertebrates is problematic if highland grassland is ancient, but easily explained by grassland recently replacing a wooded ecosystem with limited and ephemeral grass patches.

Table 1. A comparison between number of species per feeding guild, and proportion of obligate grazers, browsers, and mixed-feeders in Madagascan and East Gondwanan grasslands.

	Australia	East Africa	India	Madagascar
species per guild	22	25	11	25
mixed-feeder	23%	24%	36%	16%
browser/folivore	18%	20%	9%	80%
other	0%	0%	0%	24%
obligate grazer	59%	56%	55%	0%

(b) Comparing Madagascan and East Gondwanan herbivore guilds

When comparing the grazing-guilds of Madagascar and the three East Gondwanan subtropical grasslands, Madagascar is the outlier ($\chi^2 = 23.7$, d.f. = 3, $p < 0.0001$; table 1, electronic supplementary material, S4b). Australian, East African, and Indian herbivore guilds contain grazers comprising around 60% of species. The Madagascan subfossil mixed-feeding guild (*Aldebrachelus abrupta*, *Hippopotamus gulderbergi*, *Hadropithecus stenognathus*, and *Mesopropithecus pithecoideus*) harboured two lemur species moderately adapted to both open and forest habitats, which likely ate leaves, nuts, seeds, and fruit, although *Hadropithecus* had a mixed diet that included C₃/C₄ and crassulacean acid metabolism (CAM) plants [4]. Isotope analysis for giant tortoises revealed 16 C₃ woody-feeders, and three mixed C₃-C₄ feeders [1]. For hippos (well-represented among highland subfossils), 29 were predominant C₃ feeders, with a single mixed-feeder [1,17]. In other words, to date there is no evidence for an obligate Madagascan C₄ grazer able to exert top-down effects on a vast grassland system. In summary, the fossil record, this study, and past studies reinforce the thesis that Madagascar's endemic grasses are not grazer-dependent [7]. This missing grazing-guild advances the likelihood that a grazing niche of the sort required to foster the evolution of predominantly C₄ diets (that characterize every comparable system) was either small and transient, or absent.

(c) Highland palaeoecological record

Deglaciation 15 000 before current era (BCE) fostered replacement of ericoids by grassy woodland in the highlands, and by 7800 BCE woodland was well-established; desiccation 2000 BCE in the south-west generated higher effective moisture, lower temperatures, and highland woodland expansion [2]. About 2000 years ago, humans entered an ecosystem replete with a diverse, large-bodied megafauna (including *Aepyornis hildebrandti*, a 3 m tall, 300 kg bird, and *Archaeoin-dris fontoymontii*, a 200 kg lemur). As populations of these megafauna collapsed around 600 CE, a decline in spore-rich dung is evident in the south-west ([18], figure 2). In the highlands, this coincided with an unprecedented spike in charcoal microparticles, as woodland burned over four centuries [2]. Transformation was island-wide, as evidenced by remarkably swift and complete anthropogenic conversion between 900 and 1000 CE of north-west lowland forest to grassland during one of the region's wettest centuries [25]. The spread of Fiekona pottery across the highlands was coincident with the replacement of tree pollen by that of grasses.

By 1100, the highlands had become grassland, and fungal spores spiked as newly introduced cattle reflected the shift to pastoralism. The last vestiges of endemic megafauna disappeared from the fossil record (*Megaladapis*, a 50 kg koala lemur, 'youngest' of the highland subfossil lemurs, dates to 1200 CE), as extirpation concluded a 1000-year period of extensive subsistence hunting [23]. By 1300, villages proliferated, and dedicated agro-pastoralism that now characterizes the modern highlands, ensued. The debate around aridification or anthropogenic activity facilitating grass replacing trees is a false dichotomy. Moisture-sensitive subfossil nitrogen isotope studies confirm 10 000 years of climate stability with ordinary oscillations, and that the highlands remained relatively moist throughout the last 2000 years with no evidence for coincident aridification when grass replaced woodland [24]. The palaeoecological record affirms that endemic grasses (and the remaining woodland pockets) encountered obligate grazers, cattle, and the intensified fire regime that accompanies pasture preparation, very recently. We should therefore anticipate consequent thinning of remaining woodland as fire-resistant trees are selected, and a decline in endemic grasses relative to fire and grazing-adapted non-endemics that evolved elsewhere.

(d) Relative representation of endemic grass species under fire and grazing

Grasses with a long evolutionary history should have high levels of endemism, and inspection of the data in a study across 61 sites and 5 ecoregions, revealed only 13% of species in highland grass assemblages were narrow endemics, and that highland grass endemism was significantly lower than other ecoregions ([7], figure 3a). Evaluating data from another study [9] spanning 56 highland sites established that endemic species are excluded from dominant highland grassland grass-guilds, yet increased with woody canopy cover, accounting for 20% of species in tapia woodland-dominant grass-guilds, and 40% in remnant highland subhumid forest grass-guilds (figure 3b).

Theory predicts that fire and grazing select a suite of adapted grasses. A recent study on common grass species across 71 highland sites identified a highland fire-adapted functional group [10]. Analysis of these data showed that of a combined intermediately and fully fire-adapted functional group, only 26% were endemic, in contrast with countrywide endemism exceeding 40%. When fire-adapted grass species were evaluated for presence across sites, not a single endemic emerged in the dominant suite (figure 3c). The most 'successful' endemic species was absent from 50 of 71 sites while the

Figure 2. Multisource [2,4,13,17,18,23,24] synthesis of events impacting Madagascar highland ecology. (Online version in colour.)

most successful non-endemic was recorded at over 80% of sites. Non-endemic dominant species thus occupied 100%–280% more sites than the most successful fire-adapted endemic. As remarkable is that two-thirds of fire-adapted endemics were absent from at least 64 of 71 potential sites (greater than 90% of sites; figure 3c). Representation would have been even lower had the study not omitted the 11 most rare endemics.

The proportion of endemic grasses at highland sites increased with altitude and decreased with fire and grazing (altitude $z = 2.00$, $p = 0.04$; grazing + fire $z = -2.34$, $p = 0.027$; electronic supplementary material, S4c), supporting both island-wide grazing findings by Vorontsova *et al.* [7], and interpretation of fire-adapted grass data from Solofondranohatra *et al.* [10]. In summary, highland grasslands have the lowest regional endemism, and these endemics are disproportionately sensitive to grazing and fire. They are absent from dominant grassland guilds; of grasses identified as dominant across the highland grassland, all evolved outside of Madagascar [9]. Furthermore, endemic species are absent from the dominant fire-adapted grass assemblages at over 70% of sites sampled [10]. Despite diversifying *in situ* since the Miocene [7,8], endemic grasses lack the expected adaptive characteristics for disturbance regimes to which they are now exposed [16,22]. Much like the global domination of C_4 over C_3 grasses as spaces opened in the Miocene, recent arrivals outcompete Madagascar endemics on intensively burned cattle grazing-lawns, because these non-endemics evolved elsewhere, in ecosystems exposed to grazing and fire.

C_4 grasses need not be constrained to open space. In Madagascar for example, the oldest C_4 lineage is limited to the spiny forest, the island's most ancient biome, a stunted, partially canopied dryland with a bushy understory [8].

Moreover, C_4 grasses dominate open- and closed-canopy miombo woodland across south-central Africa [4,27], and many consider Madagascar open-canopy tapia woodland, dominated by a monoculture of *Uapaca bojeri* and C_4 grasses (with a herbaceous understory of *Sarcolaenaceae*, *Lamiaceae*, *Asteraceae*, *Rubiaceae*, and *Cyperaceae* in less disturbed areas) to be remnants of a broadly similar system [4,14,28]. Were this so, then the original assemblage, represented today by *Uapaca bojeri*, has likely relinquished key species. Such losses are best understood by comparing fire-effects in African miombo woodland. In contrast with tapia, fire-adapted miombo cannot tolerate fire intensities to which tapia are currently exposed. A telling experiment spanning three decades showed miombo fire-intolerant trees disappeared early from assemblages, followed by intermediately tolerant species (like the canopy-forming *Caesalpinioideae*: *Brachystegia*, *Julbernardia*, and *Isobertlinia*), leaving grassland with scattered fire-tolerant trees including *Uapaca kirkiana*, *U. pilosa*, and *U. nitida* [29]. Overly frequent fire is converting miombo woodland *Caesalpinioideae* to grassland, cropland, and charcoal [27,30], paralleling the prevailing transformation of Madagascar *Caesalpinioideae* in western deciduous forests. In African forests and miombo, clearance-burning initially selects fire-tolerant *Uapaca* [29]. If miombo is broadly comparable to tapia woodland [4,14], Madagascar *Uapaca bojeri* may represent fire-resistant vestiges of a once species-rich and complex woodland, having historically undergone similar anthropogenic transformation that now characterizes Madagascar's western deciduous woodland. Current conversion of miombo to grassland throughout south-central Africa illustrates that C_4 grasslands emerge quickly following deforestation [27]. Even with normal fire regimes, intensive grazing reduces miombo tree functional richness in only five

Figure 3. Percentage of narrow endemic grass species per ecoregion (a) [7]; proportion of endemic grass species in dominant highland grass-guilds across habitat (b) [9] and number of sites out of 71 that endemic (E) and non-endemic (NE) grass species belonging to a fire-adapted functional group occur (c) [10]. Map after Yoder [26]. (Online version in colour.)

decades [31]. African mainland C_4 grasses have however evolved to be grazed and burned, whereas Madagascan endemics lose ground.

Charcoal particles in the palaeoecological record show decimation of highland woodland from 600 CE. Grass pollens begin replacing those of trees, forest-dwelling megafauna disappear, and pastoralism prevails from 1100 CE. Not even during the last glaciation, and at no time since, has Madagascar been so dominated by grassland [2,4]. There is no debating the ancient existence of grassy woodland, nor of grassy patches vacillating in size with prevailing fire and climate conditions [2,4,8]. Such patches were likely small and transient, however, explaining Madagascar's almost total woodland-limited vertebrate speciation. If grasslands had been large and expansive, it is inconceivable that the adaptive radiations across habitats, as seen in Australian, African, and Indian grasslands would not have occurred.

4. Conclusion

Tavy is the pervasive cultural practice of clearing an area entirely of canopy trees and understory, letting it dry for a few weeks, and then lighting the tinder. It is illegal, and ubiquitous. These cleared areas, if not used for rice, sugar cane, coconut, maize, coffee, or ylang-ylang, are burned annually for cattle pasture. Hillsides disintegrate as erosion gullies called *lavaka* (literally 'holes', approaching 30 km² in area) spread across the highlands, and in some areas, 250 tonnes of topsoil are lost per hectare per year [4]. This enduring practice of annual burning, refined over 10 centuries, allows remnant *Uapaca bojeri* to persist only because the genus is exceptionally fire-tolerant [28]. Yet even *tapia face* extirpation

as fires impact fruit set, reproduction, recruitment, and increase mortality [28].

Several lines of evidence affirm the highland grassland is young. Lacking a megafaunal grazing-guild the system was historically maintained by low-intensity natural fires [2]. Today grassland and closed-canopy subhumid forest patches coexist only metres apart, despite no climate or soil changes [4,10], and in the absence of disturbance, forest tends to replace grassland [4,32]. This grassland, devoid of an evolutionary relationship with extant vertebrates, hides subfossil ghosts of extinct lemurs, and woodland and forest now transfigured to charcoal. It likely possessed a complex understory including a far higher proportion of endemic grasses, forming a graded continuum ranging from humid forest-related assemblages in the east, to deciduous-type forest in the west, interspersed with small grassy patches succeeding occasional, low-intensity natural fires. At the onset of the last millennium, endemic grasses may initially have spread as woodland and forest disappeared, but overall, the persistence of even those that can cope with limited grazing and intensive fires appears precarious, whereas dominant assemblages, now entirely composed of non-endemics better adapted to novel disturbance regimes, proliferate as they outcompete endemic grasses.

Data accessibility. Data are available from electronic supplementary material, S1–S4.

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