



The antiquity of Madagascar's grasslands and the rise of C₄ grassy biomes

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ABSTRACT

Aim Grasslands and savannas, which make up > 75% of Madagascar's land area, have long been viewed as anthropogenically derived after people settled on the island c. 2 ka. We investigated this hypothesis and an alternative – that the grasslands are an insular example of the post-Miocene spread of C₄ grassy biomes world-wide.

Location Madagascar, southern Africa, East Africa.

Methods We compared the number of C₄ grass genera in Madagascar with that in southern and south-central African floras. If the grasslands are recent we would expect to find fewer species and genera in Madagascar relative to Africa and for these species and genera to have very wide distribution ranges in Madagascar. Secondly, we searched Madagascan floras for the presence of endemic plant species or genera restricted to grasslands. We also searched for evidence of a grassland specialist fauna with species endemic to Madagascar. Plant and animal species endemic to C₄ grassy biomes would not be expected if these are of recent origin.

Results Madagascar has c. 88 C₄ grass genera, including six endemic genera. Excluding African genera with only one or two species, Madagascar has 86.6% of southern Africa's and 89.4% of south-central Africa's grass genera. C₄ grass species make up c. 4% of the flora of both Madagascar and southern Africa and species : genus ratios are similar (4.3 and 5.1, respectively). Turnover of grasses along geographical gradients follows similar patterns to those in South Africa, with Andropogoneae dominating in mesic biomes and Chlorideae in semi-arid grassy biomes. At least 16 monocot genera have grassland members, many of which are endemic to Madagascar. Woody species in frequently burnt savannas include both Madagascan endemics and African species. A different woody flora, mostly endemic, occurs in less frequently burnt grasslands in the central highlands, filling a similar successional niche to montane C₄ grasslands in Africa. Diverse vertebrate and invertebrate lineages have grassland specialists, including many endemic to Madagascar (e.g. termites, ants, lizards, snakes, birds and mammals). Grassland use of the extinct fauna is poorly known but carbon isotope analysis indicates that a hippo, two giant tortoises and one extinct lemur ate C₄ or CAM (crassulacean acid metabolism) plants.

Main conclusions The diversity of C₄ grass lineages in Madagascar relative to that in Africa, and the presence of plant and animal species endemic to Madagascan grassy biomes, does not fit the view that these grasslands are anthropogenically derived. We suggest that grasslands invaded Madagascar after the late Miocene, part of the world-wide expansion of C₄ grassy biomes. Madagascar provides an interesting test case for biogeographical analysis of how these novel biomes assembled, and the sources of the flora and fauna that now

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occupy them. A necessary part of such an analysis would be to establish the pre-settlement extent of the C₄ grassy biomes. Carbon isotope analysis of soil organic matter would be a feasible method for doing this.

Keywords

Africa, biome origin, C₄ grasses, deforestation, fire ecology, grassland, Madagascar, savanna.

'One has to admit that the [central plateau region of Madagascar] must have always been without trees, but not from the hand of man, since it was a vast deserted [landscape] of which not even 10% was populated.' Grandidier (1898, p. 84).

'The formation of the prairies [of Madagascar] is totally artificial and the result of fire. We would not insist on this except that some have said that the prairie, the malgache steppe, is a natural formation having existed since ancient times.' Perrier de la Bâthie (1921, pp. 9–13).

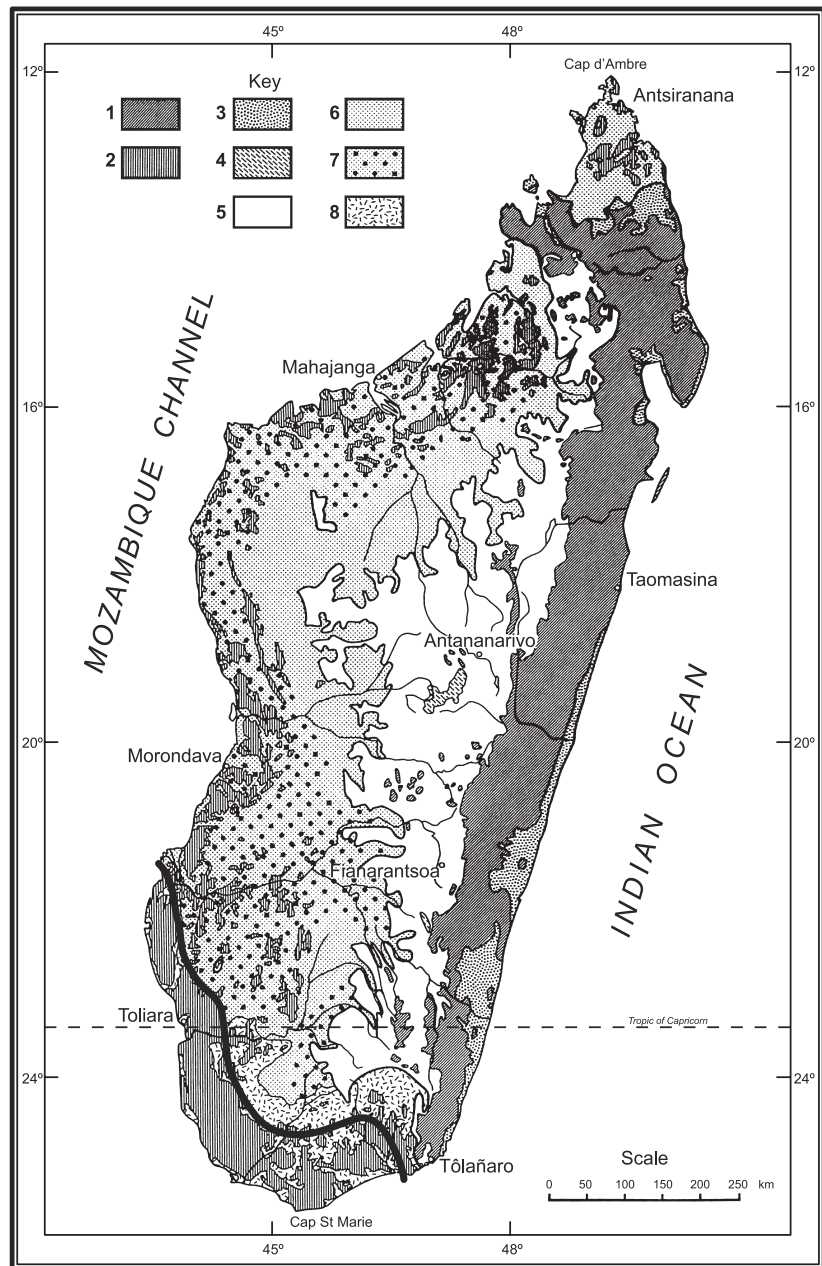
INTRODUCTION

Madagascar has the reputation of being one of the most degraded landscapes on Earth. This reputation stems, partly, from the belief that the 'original' forests, especially in the centre of the country, have been replaced by 'degraded' grasslands through human activities, particularly burning to clear the land for crops and for rearing livestock. There is well-documented evidence for deforestation over the last century in evergreen forests of eastern Madagascar (Green & Sussman, 1990; Agarwal *et al.*, 2005) and deciduous forests of western Madagascar (Smith *et al.*, 1997). However, there is continuing debate on the antiquity of grassy biomes that cover vast areas of the centre and the west of the island. Early proponents of anthropogenic origins were Humbert (1927, 1955) and Perrier de la Bâthie (1928, 1936). Indeed their particular perspective and that of many, but not all (cf. Grandidier, 1898), early French naturalists remains pervasive to this day (Lowry *et al.*, 1997; Kull, 2000, 2004; Klein, 2002). The 'degraded' grasslands are those that dominate the central highlands and the western slopes of the island (Koechlin, 1993). Evidence for their anthropogenic origin is primarily the poverty of species and the lack of endemism, contrasting sharply with the forested parts of Madagascar (Humbert, 1927; Perrier de la Bâthie, 1936; Koechlin, 1972; Koechlin *et al.*, 1974; Lowry *et al.*, 1997). Yet we find that few comparisons have been made with similar grassy ecosystems elsewhere, such as those on the African mainland. Here we return to the question of whether Madagascar's grasslands are of anthropogenic origin. We suggest, instead, that the grasslands are ancient and that many of their peculiarities are part of a wider phenomenon: the abrupt origin and rapid spread of C₄ grassy biomes world-wide over the last 7–8 million years (Myr).

In its most extreme form, the degradation hypothesis argues that Madagascar's grasslands (other than high-montane C₃-dominated grasslands, which were thought to be 'natural') originated as a result of relatively recent human occupation of the island (Humbert, 1927; Perrier de la Bâthie, 1928, 1936); humans only arrived 1500–2000 years ago (Burney *et al.*, 2004; R. Dewar, personal communication). Koechlin (1993) stated that 'human activity is directly or indirectly responsible for replacement of the original vegetation by secondary types. Forest has been destroyed by cutting of trees and by fire'. Fires promoted highly flammable grasslands which in turn promoted fire, the 'grass–fire' cycle (cf. D'Antonio & Vitousek, 1992), leading to rapid replacement of forest. However, the human population of Madagascar has been small relative to the size of the island, with only *c.* 2.5 million people in 1900, very unevenly distributed, with 'vast areas in the west almost totally uninhabited and no doubt always been so' (Koechlin, 1993). Thus Mayeur (1777, [1913]) noted vast areas of grassy landscape in the central highlands of the island without villages, people or cattle. As Koechlin (1993, p. 188) observed: 'It may be wondered how men could have cleared such extensive areas'. He goes on to suggest that Madagascar, in common with other island floras, lacked aggressive and heliophilous tree species capable of colonizing grassland. Today, grasslands, defined as landscapes with more or less continuous grass cover with or without scattered trees or patches of woody plants (Scholes & Archer, 1997), occupy *c.* 80% of the island's 587,000 km² area (Fig. 1). If these grasslands are of anthropogenic origin, this represents a remarkable transformation over 2 millennia.

The anthropogenic hypothesis for the origin of grasslands was shaken by the discovery of grass pollen and charcoal in Holocene sediments much older than 2000 years (Burney, 1987a; b). A core taken from Lake Tritrivakely in the central highlands, where forests were thought to have been replaced by anthropogenic grasslands, had abundant grass pollen, comparable to contemporary grasslands, as far back as 10 thousand years ago (ka), with charcoal exceeding contemporary amounts from 10 to 4 ka, long before human settlement (Burney, 1987a). This was subsequently confirmed by other cores taken here and elsewhere in the central highlands (Burney, 1987b; Gasse & Van Campo, 1998, 2001). Burney (1987a) noted that 'the apparent existence of open vegetation types, pyrogenic communities and shifting vegetation dominance in pre-settlement Madagascar is in direct contradiction to key aspects of the Perrier de la Bâthie–Humbert hypothesis

Figure 1 Map of the grassy formations (units 3–8) of Madagascar, modified after Koechlin *et al.* (1974, map 21, p. 444) and from Humbert & Cours-Darne (1964–65), Bosser (1969) and Rattray (1960): 1, forests of the eastern region; 2, forests/woodlands of the west, plus the south-western thicket vegetation (the thick line approximately separates the two formations); 3, savannas and grasslands of the east coast, with *Imperata cylindrica*, *Hypparrhenia rufa*, *Aristida similis*, *Panicum* spp., *Digitaria humbertii*, etc.; 4, prairies and shrublands of the high mountains (above 2000 m), with *Pentaschistis* spp., *Andropogon trichozygus*, *Digitaria* sp., *Poa* spp., *Anthoxanthum madagascariensis*, etc.; 5, grasslands and savannas of the central plateau, with *Aristida rufescens*, *Loudetia simplex*, *Trachypogon spicatus*, *Hyperthelia dissoluta*, *Ctenium concinnum*, etc.; 6, herbaceous savannas of the west, with *Heteropogon contortus*, *Hypparrhenia* spp., *Loudetia* spp., *Themeda quadrivalvis*, *Panicum* spp., etc.; 7, tree and shrub savannas of the west, with *Hypparrhenia* spp., *Chrysopogon* sp., *Imperata cylindrica*, *Neostapfiella perrieri*, *Perotis* sp., etc.; 8, savannas and steppes of the south, with *Heteropogon contortus*, *Aristida* spp., *Cenchrus ciliaris*, *Eragrostis* sp., *Panicum voeltzkowii*, etc. For a more complete list of species and a discussion of their distributions see Koechlin *et al.* (1974).



that pre-settlement Madagascar was characterized by closed ‘climax’ vegetation types’.

Despite the palaeo evidence for a long history of grasslands and pre-settlement fires in the central highlands, grasslands there are still widely seen as primarily of anthropogenic origin. For example, Lowry *et al.* (1997) explicitly questioned the significance of the pollen data in indicating extensive pre-settlement grasslands, arguing that grass pollen formed a low percentage 2 ka prior to human settlement. Their view of pre-settlement vegetation in areas currently occupied by grasslands was of a ‘mosaic of woody vegetation types (woodlands, bushland, shrubland and thicket) in which herbaceous species, including grasses, were abundant’. They accepted that small isolated pockets of edaphic grasslands may have occurred where substrate conditions were unfavourable for woody

vegetation, such as rock outcrops and wetlands. But they concluded that it is ‘unnecessary to invoke grassland as a dominant vegetation type present when humans arrived’ and explicitly called for adoption of the term ‘secondary grassland’ in favour of older, more neutral, terms such as prairie, savanna or pseudosteppe.

Most of the grasslands of the central highlands and lower elevations of Madagascar are dominated by C_4 grasses, something that has not previously been noted in the literature. C_4 photosynthesis differs from that of C_3 by the addition of a CO_2 -concentrating mechanism at the site of carboxylation. This reduces photorespiration, enabling leaves to fix more carbon than C_3 plants in warmer, open environments. C_4 plants are thought to have evolved in hot regions of the world in response to decreasing atmospheric CO_2 from the mid Tertiary (Sage,

2004; Ehleringer, 2005). C_4 grassy ecosystems can be identified by distinct carbon isotope signatures in soil carbonate and in the bones of herbivorous vertebrates. Palaeosol isotope signals indicate a geologically abrupt appearance of C_4 dominated ecosystems simultaneously in Asia, Africa and the Americas some 7–8 million years ago (Cerling *et al.*, 1997) or slightly earlier (Tipple & Pagani, 2007). Spreading very rapidly from their equatorial origins, they formed novel, grassy ecosystems where forested systems had prevailed. Explanations for the abrupt origin and rapid spread of C_4 grass biomes have variously included: decreasing atmospheric CO_2 through the Tertiary (Ehleringer *et al.*, 1997), increased aridity and more frequent fires associated with the onset of monsoonal climates in the Miocene (Keeley & Rundel, 2005) or a combination of these factors with feedbacks between them (Beerling & Osborne, 2006). The evolutionary consequences and global biogeographical patterns of the spread of C_4 grasses have hardly been explored. One remarkable feature of the C_4 grass radiation is that many grass genera, and even species, are shared between continents that are separated by wide ocean barriers – an anomaly given the recent origin of C_4 grassy ecosystems. Though C_4 grasses pre-date the appearance of C_4 grass-dominated biomes by several million years (Jacobs *et al.*, 1999; Stromberg, 2005), the spread of C_4 grasslands must have depended on long-distance dispersal of many grass lineages. Whether associated plants and animals evolved *in situ*, or spread by long-distance dispersal between different C_4 grassland regions, has been little studied.

METHODS

C_4 grassland and Madagascar

If the grasslands of Madagascar are part of the post-Miocene world-wide expansion of C_4 grasses, then their origins would be much more recent than the wooded formations which they replaced. Grassland plants and animals would have been assembled from transoceanic dispersal or from existing Madagascan lineages that were able to colonize the novel habitat. Because of their isolation from mainland sources, the expectation is that Madagascan grasslands would be less diverse than their grassland counterparts on the African mainland; it is also likely that Madagascan grasslands would be less diverse than Madagascan forests because of low structural diversity of the vegetation. Yet proponents of the anthropogenic origins of Madagascar's grasslands have pointed to these same features – low diversity and low endemism of the grassland biota, especially relative to wooded formations – as evidence of recent origins (Humbert, 1927; Perrier de la Bâthie, 1936; Koechlin, 1972, 1993; Koechlin *et al.*, 1974; Lowry *et al.*, 1997; Gautier & Goodman, 2003). To determine whether the grasslands are a few million or a few thousand years old, we used the following clues:

(1) The number of C_4 grass genera shared with representative areas of the African mainland. A large proportion shared would suggest ancient grasslands (part of the general world-

wide C_4 grass radiation where different regions share closely related taxa). If grasslands originated, or had expanded from small areas only in the last 2 thousand years (kyr), we would also expect there to be few species and genera with very wide distribution ranges across altitudinal, rainfall and edaphic gradients.

(2) The presence of endemic plant species or genera in grasslands. These would not be expected if grasslands were of recent origin or if they had only occupied small areas prior to human settlement. Some speciation, and hence the presence of taxa endemic to Madagascar, would be expected if grasslands were ancient.

(3) The presence of a grassland specialist fauna. If grasslands are of Holocene origin, the fauna would all be of forest origin, unless recently introduced by people from Africa (e.g. Koechlin, 1993). There should be no grassland specialists endemic to Madagascar but only habitat generalists, i.e. species that also occur in forest and/or wooded habitats. Grassland habitats would not have existed for long enough (a few thousand years) for an autochthonous fauna to have evolved. Exceptions might be species living in wetlands or marshes which might always have lacked forest cover. If, in contrast, grasslands are ancient, then some endemic grassland specialists might be expected alongside species that dispersed to Madagascar from grassland habitats from mainland Africa or elsewhere.

We discuss available data for the grassland flora and fauna in the light of these predictions supplemented by our own observations on a small sample of grassland plots from the central highlands and south-western arid savannas of Madagascar. We interpret 'grasslands' broadly to include both grasslands and wooded grasslands (savannas) with a continuous C_4 grass matrix (Fig. 1; units 3–8).

Floral and faunal surveys

We assembled plant and animal distribution records for Madagascar and southern Africa from a variety of published and online sources. Grassy biomes have been poorly surveyed relative to other biomes in Madagascar, perhaps because of the perception that they are 'degraded'. In the absence of a recent revision of Poaceae for Madagascar, we based our list of grass taxa on Bosser (1969), the Missouri Botanical Garden data base (Missouri Botanical Garden, 2006) and the Kew data base for world grasses (Clayton *et al.*, 2007). Unfortunately the lists are not complete. For example, we examined collections of two C_4 genera, *Harpechloa* and *Monocymbium*, housed in Herbarium Tsimbazaza, neither of which is listed in Bosser (1969) or Missouri Botanical Garden (2006). Listing of the number of species and number of endemics is particularly difficult because of changing taxonomic concepts. Our analysis is therefore a preliminary one. We compared C_4 grass genera from Madagascar (587,000 km²) with the C_4 grass genera for southern Africa (area 2,675,425 km²; Gibbs-Russell *et al.*, 1990) and *Flora Zambesiaca* (area 2,740,000 km², south-central Africa; Fernandes *et al.*, 1971; Launert & Pope, 1989; Pope, 1999; Pope & Martins, 2002) to test whether Madagascar

has a depauperate flora (as predicted if the grasslands are secondary). Data on global distribution, photosynthetic pathway and current taxonomic status of each genus were obtained from Gibbs-Russell *et al.* (1990) and Watson & Dallwitz (1992). In determining which elements of the Madagascar fauna occur in grassy ecosystems, we relied heavily on the recent volume on Madagascar biota edited by Goodman & Benstead (2003).

RESULTS

The grass flora

Madagascar has 136 grass genera according to the Missouri Botanical Garden (2006) list, of which nearly two-thirds (88) have C₄ photosynthesis (see Appendix). This figure (incomplete) has not been previously reported in the literature. The number of C₄ genera is not dissimilar to that in southern Africa (with an area *c.* 4.5 times larger) with 110 listed by Gibbs-Russell *et al.* (1990), and *Flora Zambesiaca* (*c.* 4.7 times larger) with 124 genera. Madagascar shares 71 of these genera with southern Africa (64.5%) and 76 (61.3%) with *Flora Zambesiaca*. Of the genera not shared, 28 of the southern African and 39 of the *Flora Zambesiaca* genera contain only one or two species. With these smaller genera excluded, Madagascar shares 86.6% of its C₄ grass genera with southern Africa and 89.4% with south-central Africa.

Estimates of the number of species are difficult given the current state of grass taxonomy in Madagascar. As a rough indication, Bosser (1969) listed *c.* 500 species of which *c.* 350 are C₄. Kew (Clayton *et al.*, 2007) lists 482 grass species compared with 907 species for southern Africa. In both cases this represents *c.* 4% of the total flora (assuming *c.* 22,000 for southern Africa and *c.* 12,000 for Madagascar). Approximately 66% of South Africa's grass species are C₄, while the number for Madagascar is *c.* 73%. The species : genus ratios of C₄ genera for the two regions are also similar: 5.1 for South Africa and 4.3 for Madagascar. We could find no information on species endemism for grasses. Estimates of endemic genera are also difficult because of changing taxonomy. Bosser (1969) listed 16 endemic grass genera, of which eight were C₄. Taxonomic changes have reduced these to *c.* 6 (Missouri Botanical Garden, 2006): *Daknopholis*, *Decaryella*, *Neostapfiella*, *Sclerodactylon* (also on Aldabra and Assumption islands), *Viguiereella* and *Yvesia*. All of these are monotypic except *Neostapfiella*, which has three species. They belong to the Chloridae, Panicoideae (Arundinellae and Paniceae) and Andropogoninae, all major C₄ clades. The endemics occur in semi-arid, open, savanna sites with some also as halophytes in coastal areas. By contrast, the C₃ endemics include four bamboo genera (Bambuseae) and four Paniceae, mostly from shady forest habitats (Watson & Dallwitz, 1992).

The above comparisons indicate that Madagascar has a large, representative collection of C₄ grass clades, comparable with that of Africa where C₄ grassy ecosystems are the dominant plant cover. In addition, there is a significant

endemic component of C₄ grass genera. Although the grass flora needs updating, the long list of C₄ genera does not indicate a recent origin for grassy ecosystems in Madagascar. Instead, it suggests that the island was subjected to the general expansion of C₄ grasses that occurred world-wide from tropical latitudes since the late Miocene. It is striking that, rather than weedy and adventive, Madagascar has a balanced C₄ grass flora with good representation of Andropogoneae in wetter regions and Chloridae in drier regions (Fig. 1), matching similar patterns in southern Africa (e.g. Gibbs-Russell, 1988) and world-wide (Hartley, 1958; Barkworth & Capels, 2000). Both genera and species turn over along rainfall gradients in a predictable manner, a pattern that would not be expected if grasses had recently invaded forested landscapes as adventives following human clearing by felling or burning. For example, genera of Andropogoninae (*Andropogon*, *Cymbopogon*, *Hyparrhenia*, *Hyperthelia*, *Monocymbium*, *Shizachyrium*, *Trachypogon*, etc.) are common in the high-rainfall, frequently burnt grasslands of the central highlands (or seasonally wet grasslands in the west; Koechlin, 1972, 1993), just as they are in the 'highveld' of South Africa where the humid climate should support forest (Gibbs-Russell, 1988; Bond *et al.*, 2003). Species belonging to the Chloridae (*Chloris*, *Cynodon*, *Dactyloctenium*, *Perotis*, *Pogonarthria*, *Tragus*) are more common in the semi-arid grasslands and savannas of Madagascar (Koechlin, 1993), just as they are in South Africa (Gibbs-Russell, 1988) and elsewhere in the world (Hartley, 1958; Barkworth & Capels, 2000). Within the Paniceae, different genera occur in mesic (*Alloteropsis*, *Tristachya*) and semi-arid (*Cenchrus*, *Urochloa*) grasslands, following the same pattern as in South Africa.

The balanced nature of the grass flora is also evident in species turnover at smaller spatial and temporal scales. In Madagascar, Koechlin (1972, figure 7) noted fine-scale turnover of C₄ grass species along soil catenas, and heavy grazing caused more palatable Andropogoneae to be replaced by *Aristida* species (Koechlin, 1993). Similar successional trends occur in the mesic grasslands of South Africa, though with different suites of species (Tainton, 1999). In Africa and elsewhere, fire frequency is an important determinant of grass species composition in C₄ grasslands. Grasslands are often dominated by fire-dependent grass species, typically members of the Andropogoneae. These species are fire-dependent in the sense that they decrease in, or disappear from, a sward in the absence of frequent burning. For example, *Themeda triandra* decreased from > 70% cover in frequently burnt South African grasslands to < 10% when fires were excluded for 4 years or more (Uys *et al.*, 2004). These fire-dependent grasses accumulate standing dead litter which shades out and kills shade-intolerant new tillers (Knapp & Seastedt, 1986; Everson *et al.*, 1988). Though fire-driven grassland succession has yet to be studied in Madagascar, the presence of typical fire-dependent species, especially in the central highlands, is incompatible with scenarios of pristine, fire-free wooded or forested vegetation (Perrier de la Bâthie, 1936; Lowry *et al.*, 1997).

The non-grass flora

Following grasses, sedges (Cyperaceae) have the most C_4 species world-wide (Sage, 2004). Madagascar has some 34 genera and 318 species of Cyperaceae (Chermezon, 1937; Govaerts *et al.*, 2006; Missouri Botanical Garden, 2006). Twenty of the genera have only C_3 members, 10 exclusively C_4 and four genera have both C_3 and C_4 species (Soros & Bruhl, 2000; Stock *et al.*, 2004; M. Muasya, personal communication, 2006). This is comparable to the sedge flora of Natal (now Kwa-Zulu-Natal, area *c.* 95,000 km²), South Africa, with 26 genera and 224 species (Gordon-Gray, 1995) and of East Africa with 29 genera and *c.* 500 species (Haines & Lye, 1983). All 14 of the Madagascan genera with C_4 species occur in East Africa with fewer, 11, shared with subtropical Natal. Thus, as for C_4 grasses, the generic richness of the C_4 sedge flora in Madagascar is comparable to that of mainland Africa in diversity and composition. However, the inference that high generic richness indicates ancient grassland origins is not as strong as for grasses. The ecological correlates of the distribution of C_4 sedges are complex and poorly understood (Stock *et al.*, 2004). Although some C_4 sedges are components of dryland grasslands, many occur in wetlands or marshes which might always have lacked forest cover.

Grasslands represent a hostile habitat for forbs (non-graminoid herbs). To colonize grasslands, forbs of forest origin would have to contend with sunlit, seasonally dry, frequently burnt habitats with vigorous grass competitors. Thus, if grasslands are anthropogenic, very few native forbs would be expected. Yet a surprising feature of Madagascan grasslands is the common presence of forbs. In a small ($n = 7$) sample of grassland relevés in the Central Plateau, we counted an average of 12 grass species (range 8–16) and 12 (range 8–18) non-grass forb species per plot. The forbs included both monocots and dicots; some were geophytes with swollen underground storage organs that facilitate resprouting after fire.

We searched the *Flore de Madagascar* accounts of several monocot families (Humbert & Leroy, 1936–2002; Goldblatt, 1989; for Iridaceae) for species occurring in grasslands. Genera with grassland representatives (*indicates including grassland species endemic to Madagascar) include (Iridaceae) **Aristea*, **Gladiolus*; (Orchidaceae) **Benthamia*, *Brachyorythis*, **Cynorkis* (= *Cynosorchis* in Perrier de la Bathie), **Disa*, **Diplaorchis* (now *Brachyorychthis*), **Lissochilus* (now *Eulophia*), **Habenaria*, **Nervilia*, **Satyrium* and **Tilostigma*; (Hypoxidaceae) *Hypoxis*; (Commelinaceae) **Commelina*; and (Hyacinthaceae) *Rhodocodon*, *Hyacinthus*. The forb flora includes both grassland species present in Africa (e.g. members of *Disa*, *Gladiolus* and *Hypoxis*) and a substantial endemic component. The presence of numerous grassland-endemic forb species from diverse genera in several families is not consistent with a recent origin for these grasslands. We could find only one published study of forb diversity in a grassland. Rabataliana *et al.* (1999) surveyed the montane grassland flora of Andringitra National Park in the central highlands and found 30+ species of ground orchids.

The grasslands are at the higher altitudinal limit of C_4 -dominated systems and include C_3 (*Pentstemon*) as well as the dominant C_4 genera (*Sporobolus*, *Imperata*, *Craspedorhachis* and *Rytachne*). They note that the orchids ‘colonize sites...clearly favoured by...the conditions of an open short-grass prairie resulting from the “sustainable disturbance” of fires and grazing’. Indeed, the authors argue that biodiversity conservation of these grasslands depends on specific fire management regimes. More surveys of forbs are needed to determine diversity and turn-over in different grassland types.

Grassland trees

The absence of trees in the grasslands of the central highlands of Madagascar (Fig. 2a) has been attributed to their anthropogenic origin. However, similar gradients from wooded savannas at lower elevations to treeless C_4 grasslands at cooler, high elevations (Fig. 2b) are the norm across east to southern Africa (Acocks, 1953; Meadows & Linder, 1993; O’Connor &

(a)



(b)



Figure 2 Grassland–forest mosaics in (a) the central highlands of Madagascar and (b) the highlands of Kwa-Zulu Natal, South Africa. The grasslands of both areas are made up of C_4 species and both burn at 1- to 3-year intervals. Palaeo-ecological studies indicate that African grasslands, such as those illustrated, are ancient and were even more extensive in the last glacial, long before humans began to clear forest for cultivation (see text).

Bredenkamp, 1997). Fire-tolerant savanna trees in Madagascar include both endemic species (e.g. *Stereospermum variabile*, *Dicoma incana*, *Acridocarpus excelsa*, *Uapaca bojeri* and the palms *Hyphaene shatan*, *Bismarckia nobilis* and *Borassus madagascariensis*), plus some species, perhaps introduced, that are widespread in Africa (e.g. *Ziziphus mauritianus*, *Sclerocarya caffra* = *Poupartia caffra*; Koechlin, 1972, 1993).

One noteworthy savanna ecosystem found scattered across the central highlands is the 'tapia' woodland, dominated by *Uapaca bojeri*, and other endemic fire-tolerant tree species (including *Uapaca densifolia*, *Agauria salicifolia*, *Asteropeia densiflora*, *Cussonia bojeri*, *Leptolaena bojeriana*, *Sarcolaena oblongata* and others; Gage, 1985). A diversity of C₄ grasses and C₃ forbs (including geophytes) occurs in the grass matrix layer (Kull, 2003). As Grubb (2003) noted, these woodlands are strongly reminiscent of miombo formations in Africa, which are also mesic savanna woodlands with a frequently burnt, C₄ grassy understorey. *Uapaca* species are common in miombo woodlands but some species, in both Africa and Madagascar, are restricted to closed forests which lack grass-fuelled fires. Molecular studies might help indicate whether the *Uapaca* species in Madagascar's tapia woodlands are derived from fire-tolerant African savanna lineages or evolved from Madagascan forest clades.

Another suite of heliophytic woody species also occurs in the mesic grasslands of the central highlands. These are found colonizing infrequently burnt grasslands and along forest margins. Species include *Harungana madagascariensis*, *Trema orientalis*, *Agauria* spp., *Dodonaea madagascariensis*, *Filicium decipiens*, *Rhus taratana* and species of *Croton*, *Dombeya*, *Macaranga* and *Erica* (Lowry *et al.*, 1997; Parelissen *et al.*, 2006). Many of these forest-edge species readily resprout from roots or epicormic buds following fires (personal observation). Others such as *Erica* are iconic species of fire-prone landscapes (White, 1983). Some species, such as *Trema orientalis*, also occur in Africa. Most are native to Madagascar but fill a similar successional niche of shade-intolerant forest/grassland ecotonal sites to their congeners in Africa (Acocks, 1953; O'Connor & Bredenkamp, 1997).

The grassland fauna

Table 1 provides a summary of grassland (including savanna) vertebrates and invertebrates extracted from Goodman & Benstead (2003). In diverse invertebrate and vertebrate groups, there are distinct grassland specialists together with species that use grassland/forest margins. The grassland specialists include many species endemic to Madagascar such as termites, ants (Fisher & Robertson, 2002), lizards (even a chameleon!), snakes, birds and mammals (several species of tenrecs, Goodman *et al.*, 2003; Tingle *et al.*, 2003). In nearly all groups, the grasslands have far fewer species than forests (but see Fisher & Robertson, 2002, for ants). In several instances, grassland species have stronger phylogenetic connections to Afro-Asian clades than to Madagascan ones. For example, the grass-dwelling snake *Mimophis mahafalensis* is more closely

related to Afro-Asian *Psammophis* than all other Madagascan colubrids (Cadle, 2003). The Madagascar fody, *Foudia madagascariensis*, is a gregarious, granivorous bird apparently related to African queleas and euplectids (Craig, 2003). Caddis flies (Trichoptera) fall into two distinct groups, endemic forest dwellers, and widespread grassland/savanna species with African affinities (Gibson, 2003). Many endemic grassland birds have close affinities with Afro-Asian species (e.g. Madagascar bush lark, *Mirafra hova*; Madagascar cisticola, *Cisticola cherina*; Madagascar buttonquail, *Turnix nigricollis*; and Madagascar partridge *Margaroperdix madagascariensis*). However, some grass habitat users include species from distinctive Madagascan 'forest' clades, such as Chabert's vanga *Leptopterus chabert*, which is a common group forager in savannas (Tingle *et al.*, 2003). We believe that invertebrates in particular have been vastly under-collected and inventoried in grassland systems (cf. Fisher & Robertson, 2002) such that the level of diversity and endemism remains unknown.

Vertebrate grazer assemblages – the subfossil fauna

Madagascar had a diverse vertebrate herbivore assemblage of extinct primates, hippos, elephant birds and giant tortoises (Dewar, 1984). Did this include a grazer assemblage analogous to the African megafauna? Dewar (1984) suggested that the vegetation of the highlands must have been a mosaic of forest and open habitats to account for the observed vertebrate diversity. Burney *et al.* (2003) used *Sporormiella* spores as proxies to trace pre-settlement vertebrate herbivore biomass in Madagascar. They found evidence for high animal biomass in arid sites in south-western Madagascar, very low biomass in rain forest sites, and generally low to occasionally moderate presence in the central highlands. They suggest that components of the megafauna were well adapted to open country based on 'coeval pollen data and inferences from comparison to their living relatives elsewhere in the world'. This hypothesis raises the intriguing possibility of an independent origin of a C₄ grazer assemblage in Madagascan vertebrate clades. However, the fossil record from North America and Africa suggests that C₄ grassy biomes were initially hostile habitats for grazers. Equid diversity declined with the appearance of C₄ vegetation in North America (MacFadden, 2000) and bovid (antelope) radiation in Africa lagged several million years after the spread of C₄ grassy biomes with significant numbers of grazers only appearing after 3 Myr BP (deMenocal, 2004). It would thus be surprising to find significant numbers of grazers in the Madagascan megafauna, unless they dispersed there from Africa. Unfortunately there is no Cenozoic fossil vertebrate record for Madagascar and the diet of the subfossil fauna (all Holocene in origin) is poorly known.

Among potential grazers, hippos are prime candidates. Madagascan hippos are thought to be members of the derived genus *Hippopotamus*, which evolved during the early Pliocene in Africa and became frequent and widespread there only after 3 Myr BP (Stuenes, 1989; Boissarie, 2004). If any Madagascan hippos were grazers, their diet may thus have been ancestral,

Table 1 List of faunal groups associated with grassy habitat in Madagascar. *n*, where given, is the number of species occurring in grassland listed in the sources (see Notes column). Grassland affinity indicates whether the species are restricted to grasslands or occur in other habitats. Endemism indicates the number of species restricted to grasslands and the number endemic to Madagascar. For example, 1/15 indicates one species restricted to grassy habitats out of a total of 15 species in Madagascar (all endemic). The Notes column gives sources (authors of chapters in Goodman & Benstead, 2003) and additional information

	Genera	<i>n</i>	Grassland affinity	Endemism	Notes
Invertebrates					
Isoptera, termites	<i>Odontotermes</i>	1	Restricted	1/1	Eggleton & Davies (2003), p. 656, Table 8.25 Table 8.25
	<i>Microcotermes</i>	4	Restricted	4/20	
	<i>Nasutitermes</i>	1	Restricted	1/15	
	<i>Coarctotermes</i>	1	Restricted	1/4	<i>C. clepsydra</i> extremely abundant in savanna
Trichoptera, caddis flies		Many species		Few, if any endemic to grassland	<i>c.</i> 6% of termite species endemic to grasslands? Widespread taxa in grassland, directly affiliated with Africa, Asia suggesting recent dispersal?
Hymenoptera: ants		18	Many restricted	18/31	Forest taxa ancient and endemic (Gibson, 2003) Fisher & Robertson (2002) noted anomalously high ant endemism in 'recent' grassland
Vertebrates					
Frogs	<i>Ptychadena</i>	6	Some restricted	4/26	Vallan (2003) Forest fragmentation study
	<i>Scaphiophryne</i>	1	Restricted	1/0	Vences <i>et al.</i> (2003) Mascarene grass frog. Common in grasslands. Closely allied to African species
Lizards		2	?	?	Tingle <i>et al.</i> (2003) Common in rainy season in savannas
Chamaeleonidae	<i>Furcifer</i>	4	Restricted	4/18	Raselimanana & Rakotomalala (2003)
	<i>Paroedura picta</i>	1	?	4/66 all chameleons	Tingle <i>et al.</i> (2003) <i>F. lateralis</i> in savanna sites
Geckoes	<i>Amphiglossus</i>	1	0?	0?	Tingle <i>et al.</i> (2003) Gecko found in grassland
Skinks	<i>Mabuya</i>	6	4 restricted, 2 grass/forest	4/14	Open habitat near forest (Raselimanana & Rakotomalala, 2003) Raselimanana & Rakotomalala (2003)
Iguanidae	<i>Chalarodon</i>	1	?	?	Tingle <i>et al.</i> (2003) <i>M. elegans</i> in grasslands Tingle <i>et al.</i> (2003) <i>C. madagascariensis</i> in grasslands

Table 1 continued

Genera	<i>n</i>	Grassland affinity	Endemism	Notes
Snakes				
Colubridae				
<i>Mimophis</i>	1	Restricted	1/1	Cadle (2003) Different from all other Madagascar colubrids
<i>Liopholidophis</i>	2	Forest/grass	0/2	Cadle (2003)
<i>Liophidium</i> cf. <i>rhodogaster</i>	1	Restricted?	1/1?	Cadle (2003)
<i>Dromicodryas</i>	1	Forest/open	0/1	Only in open habitats Cadle (2003)
Aves: birds				
Grassland	29	29/283 restricted	28% Madagascar endemics	Often associated with ant nests Hawkins & Goodman (2003)
Grass/forest	22	22/283 restricted	50% Madagascar endemics	10% of avifauna restricted to grasslands Hawkins & Goodman (2003)
Both	51		19/51	Additional 22 species at home on forest/grass edges 18% of Madagascar avifauna uses grasslands. 19 of these species are Madagascar endemics
Mammals				
Tenrecs				
Spiny tenrecs		Open savanna	Endemic	Goodman <i>et al.</i> (2003) introduction Tingle <i>et al.</i> (2003) report three tenrec species in grasslands, one of which was forest edge
Rodents				
Oryzorictines		Marshes, rice fields, open areas	Endemic	
<i>Brachyuromys</i>		Wet meadows, rice fields	Endemic	High montane meadows. Not C ₄ grasslands?

from animals that crossed the Mozambique Channel in the last few million years, and contingent on the presence of adequate grass forage. Carbon isotope values (*ex Burney et al.*, 2004) indicate a pure C₄ diet for some specimens of *Hippopotamus laloumena* ($\delta^{13}\text{C}$ of collagen $> -9\text{‰}$) consistent with the grazing habit of extant African *Hippopotamus amphibius* from Africa. However, *Hippopotamus lemerlei* from western and west-central Madagascar may well have been a browser ($\delta^{13}\text{C}$ collagen -21.57 to -31.8‰). Though Madagascar's subfossil lemurs may have utilized grasslands, detailed analyses of their diet based on dental wear indicate that none were grazers (Godfrey *et al.*, 2005). The diet of one species, *Hadropithecus stenognathus*, is enigmatic. The wear patterns indicate a diet of seeds and other hard material yet the carbon isotope values indicate a predominantly C₄ diet ($\delta^{13}\text{C}$ collagen -8.4 to -13.2‰). Godfrey *et al.* (2005) suggest that the species may have eaten some grass but was not a specialized graminivore and may also have fed on plants of CAM (crassulacean acid metabolism) origin or on invertebrates that fed on C₄ dietary material. We suggest they may also have fed on the seeds of C₄ grasses. Two sympatric giant tortoises occurred in Madagascar which, according to carbon isotopic analysis, had different diets (Burleigh & Arnold, 1986), with *Geochelone abrupta* being a browser and *Geochelone grandidieri* eating a high proportion of C₄ plant material, including either grass or CAM succulents, or both. Finally, various species of elephant birds (Aepyornithidae) roamed widely in Madagascar. Clarke (2005), using eggshell fragments, found that the elephant bird, *Aepyornis maximus*, was a browser, not a grazer, in the thickets of southern Madagascar. Aepyornithids may have been common in the central highlands where the birds would have had access to more extensive grasslands than in the southern thicket region – if grasslands are ancient. Their diet has yet to be analysed, but one *Aepyornis* sp. tibiotarsus from the central highlands indicated a C₄ grass diet based on $\delta^{13}\text{C}$ values (Burney *et al.*, 2004). The problem remains that C-isotope data exist for only a couple of specimens across all species from the grassy centre of the island.

As yet, there are insufficient data to reject or accept the hypothesis of Burney *et al.* (2003) that a large grazer assemblage utilized C₄ grasslands in the central highlands. There is a need for more systematic studies on diet reconstruction of Madagascan hippos, aepyornithids and tortoises to determine whether a megafaunal grazer assemblage existed, and where they foraged on the island. Independent evolution of an insular grazer assemblage is of particular interest given the initially slow evolution of C₄ grazers in Africa (deMenocal, 2004).

DISCUSSION

We explored three sets of evidence for the antiquity of C₄ grasslands in Madagascar: (1) the diversity of grass lineages (genera and species) relative to that in Africa, and the presence of (2) plant and (3) animal species endemic to Madagascar grasslands. Other areas of the world invaded by non-native grasses (Great Basin deserts, Novak & Mack, 2001; California,

Seabloom *et al.*, 2003; Hawaii, Gange & Cuddihy, 1990) are characterized by large, monotonous expanses dominated by one or a couple of alien grasses with no ecological differentiation. In contrast, Madagascar has a balanced grass flora matching southern African C₄ grasslands in generic, species, functional and ecological diversity. There are fire-dependent bunch grasses in the central highlands of Madagascar, grazing-tolerant lawn species in the semi-arid lowlands, mesic species, arid species and everything in between. There are endemic genera and, we estimate (from species first described by Camus and Bosser in Bosser, 1969), more than 80 endemic C₄ grass species from diverse habitats. In addition, there are endemic grassland forbs, and endemic grass-associated shrubs and trees with different species assemblages in lowland and upland habitats. In one locality alone, > 30 species of ground orchids may be found (Rabataliana *et al.*, 1999) all dependent on periodic fires maintaining an open prairie. The grassland fauna tells a similar story. Fisher & Robertson (2002) found diverse endemic ant species restricted to grasslands and noted that this contradicted the prevailing view that the grasslands are of anthropogenic origin. Many other vertebrate and invertebrate groups have endemic grassland specialists (Table 1). A fourth line of evidence, palynological studies, has shown that grass pollen and charcoal preceded human settlement by thousands of years (Burney, 1987a,b). A recent study (Gasse & Van Campo, 2001) has pushed back the presence of grassy biomes at Lake Tritrivakely in the central highlands to an estimated 125 ka, with charcoal throughout! Moreover, throughout this period grasses alternated with pyrogenic Ericaceae for dominance of the system, with only short periods of dominance by woodland or forest species (Gasse & Van Campo, 2001).

None of these lines of evidence supports the idea of anthropogenic origins of the C₄ grasslands. Nor do they support the notion of small edaphic grasslands from which the nucleus of a grassland biota spread across the island. The grasses are far too diverse and specialized to particular habitats, and even different successional states within habitats, to have originated from edaphic islands. It is also very unlikely that C₄ grasses occurred only in the understorey of wooded formations, as suggested by Perrier de la Bâthie (1936) and reiterated by Lowry *et al.* (1997). The C₄ grasses in the central highlands are simply not shade tolerant. So much so that their close relatives in other parts of the world shade themselves out by accumulating undecomposed litter in the absence of frequent burning (Knapp & Seastedt, 1986; Everson *et al.*, 1988).

We envisage pre-settlement grasslands in Madagascar looking much as they do today in the less populated areas of the island. Analogous landscapes and grassy formations occur in southern and eastern Africa (Cowling & Richardson, 1997). Of particular interest are the extensive grasslands in the mesic, summer-rainfall, higher-altitude regions in the east of southern Africa. Here, too, the grasslands are treeless but forest patches occur in fire refugia (Fig. 2). There are also strong parallels in ecological interpretations of the origins of these grasslands (Ellery & Mentis, 1992; Bond *et al.*, 2003). They were also thought to be of anthropogenic origin – created by felling and

burning when farmers settled the area also *c.* 2 ka (Acocks, 1953). In parallel with Madagascar (Burney, 1987a, 1997; Gasse & Van Campo, 1998, 2001), the pollen record shows that grasslands are much older than originally thought in southern Africa (Meadows & Linder, 1993) and, indeed, were most extensive in the last glacial when human populations were very small but fires continued unabated (Scott, 2002a,b). Belated recognition of the many endemic species in the grassland flora and some elements of the fauna has led to intense conservation interest in the surviving remnants in southern Africa (Cowling & Hilton-Taylor, 1997; Bond *et al.*, 2003). The same has yet to happen in Madagascar.

Confusion as to the origin of C₄ grasslands has been widespread in many parts of the world for most of the past century. The problem seems to stem from the anomalous presence of grasslands in climates that can support forests, and also from the assumption that the fires that maintain the grasslands must be of anthropogenic origin. We now know that C₄ grassy biomes *are* an anomaly, but a much more ancient one: indeed, one that pre-dates hominids, never mind their use of fire. They appeared in a world with low atmospheric CO₂ and their rapid spread was accompanied by an apparent exponential increase in biomass burning as indicated by charcoal in marine sediments (Keeley & Rundel, 2005; Beerling & Osborne, 2006). The consequences for the biota seem to have been devastating. The diversity of grazing mammals decreased after C₄ grassy biomes appeared in North America (MacFadden, 2000). African bovids (antelope) only began to diversify 3 or 4 Myr after grasslands appeared (Vrba, 1985; deMenocal, 2004), coincident with radiation of the hippo lineage from which Madagascan hippos are derived. Trees may also have been slow to colonize C₄ grasslands. Carbon isotope analyses indicate that present-day elephants are predominantly browsers, but the browsing habit is < 1 Myr old suggesting that too few savanna trees were available to support browsing elephantids before then (Cerling *et al.*, 1999).

Though poorly studied, there are some curious paradoxes in the assembly of C₄ floras. The common grass genera (and some species) are cosmopolitan, suggesting extraordinary dispersal ability. However, dominant savanna trees come from different lineages in different regions: eucalypts in Australia, acacias and caesalpinoids in Africa, dipterocarps in south-east Asia, and diverse taxa in South America (Bond *et al.*, 2005). Unlike the grasses, this suggests local evolution of grass- and fire-tolerant trees from ancestral wooded formations in each region. The origins and affinities of the forb flora in different C₄ regions have yet to be studied. Madagascar is well placed to provide insights into the assembly of a C₄ grass biota. The isolation of the island has long been emphasized as a major factor in the development of its unique biota. Recent molecular studies point to dispersal, rather than vicariance, as the source of several distinctive elements of the fauna (Yoder & Nowak, 2006). Vicariance cannot explain the sources of C₄ grassland biota: the biome is too young. But it should be possible to distinguish origins through dispersal from Africa (or further

afield?) vs. speciation from pre-existing Madagascan sources. It would be fascinating and revealing to determine which kinds of organisms have had the least, and which the most, difficulty in colonizing this novel ecosystem.

Anthropogenic impacts

Though we have argued that Madagascan grassy biomes are ancient, human activity may have greatly increased their extent. Current deforestation and slash and burn agriculture are transforming the ecosystems of Madagascar (Green & Sussman, 1990; Smith *et al.*, 1997; Agarwal *et al.*, 2005). How much did they do so in earlier centuries? Felling of forests, slash and burn agriculture, and especially fire, were thought to have led to the replacement of forests by C₄ grasslands and savannas world-wide. Yet in Africa, forests are far more extensive now than they were in the last glacial when human pressures were low but fires continued to burn (Ehleringer *et al.*, 1997; Wooller *et al.*, 2000; Scott, 2002a,b). There is very little quantification of the scale of human impacts anywhere. Human settlement of Madagascar, at *c.* 2 ka, is more recent than for any other large area of C₄ grassland. Traces of pre-settlement forest should still be present as organic matter in the deeper layers of contemporary grassland soils and could be identified by their carbon isotope signal. Switches from forest to C₄ grassland can be recorded in soil organic matter that can be radiocarbon dated (Trumbore, 2000; Schwartz *et al.*, 2004) although the dates are less reliable than those derived from depositional material. The advantage of the isotope method is that soils can be sampled anywhere in the landscape where they are deep enough to observe the transitions of interest. We conducted preliminary analyses from several sites in the central highlands and eastern mountains with promising results. One grassland site showed very recent conversion from forest to grassland, others showed more ancient conversion, and some had remained grassland throughout the period represented by the entire soil profile (W. Bond, J. Silander & E. February, in preparation). More extensive sampling could reveal, for the first time anywhere, the true extent of anthropogenic conversion of forest to C₄ grassland.

CONCLUSIONS

Neither biogeographical nor palynological evidence (Burney, 1987a, 1997; Gasse & Van Campo, 1998, 2001) supports the widely held notion that the grassy biomes of Madagascar are of recent (< 2 ka) origin. We suggest that biologists should take a fresh look at Madagascan grasslands, not least because the grassland biota has been largely neglected in biological inventories for conservation in a country characterized by almost unparalleled levels of endemism. Grassy ecosystems in general have been viewed as an alien, rather than intrinsic, component of this extraordinary island. We think Madagascar can also contribute significantly to a general understanding of the biogeography and assembly of tropical grasslands. The insular context can help provide unique perspectives on the

world's newest 'abominable mystery' – the abrupt origin and rapid expansion of the C₄ grasslands.

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APPENDIX

List of C₄ grass genera in Madagascar showing genera shared with southern Africa (Gibbs-Russell *et al.*, 1990) and tropical Africa and Asia (from Clayton *et al.*, 2007; and Missouri Botanical Garden, 2006). Genera with an asterisk are listed in Missouri Botanical Garden (2006) but not in Clayton *et al.* (2007). Genera in bold are not listed in either database (see text).

Endemic	Shared with			
	Southern Africa			Rest of Africa/Asia
<i>Daknopholis*</i>	<i>Acrachne</i>	<i>Eriochloa</i>	<i>Schoenefeldia</i>	<i>Crypsis</i>
<i>Decaryella</i>	<i>Alloteropsis</i>	<i>Eulalia</i>	<i>Setaria</i>	<i>Dimeria</i>
<i>Neostapfiella</i>	<i>Andropogon</i>	<i>Hackelochloa</i>	<i>Sorghastrum</i>	<i>Euclasta</i>
<i>Sclerodactylon</i>	<i>Aristida</i>	<i>Harpochloa</i>	<i>Sorghum</i>	<i>Garnotia</i>
<i>Viguiereella</i>	<i>Arthraxon</i>	<i>Hemarthria</i>	<i>Sporobolus</i>	<i>Halopyrum</i>
<i>Yvesia</i>	<i>Arundinella</i>	<i>Heteropogon</i>	<i>Stenotaphrum</i>	<i>Heteropholis</i>
	<i>Axonopus</i>	<i>Hyparrhenia</i>	<i>Themeda</i>	<i>Neyraudia</i>
	<i>Bothriochloa</i>	<i>Hyperthelia</i>	<i>Trachypogon</i>	<i>Saccharum</i>
	<i>Brachiaria</i>	<i>Imperata</i>	<i>Tragus</i>	<i>Thuarea</i>
	<i>Cenchrus</i>	<i>Ischaemum</i>	<i>Tricholaena</i>	<i>Tripsacum</i>
	<i>Chloris</i>	<i>Leptocarydion</i>	<i>Trichopteryx</i>	<i>Zoysia</i>
	<i>Chrysopogon</i>	<i>Leptochloa</i>	<i>Tripogon</i>	
	<i>Coix</i>	<i>Lepturus</i>	<i>Tristachya</i>	
	<i>Craspedorhachis</i>	<i>Loudetia</i>	<i>Urelytrum</i>	
	<i>Ctenium</i>	<i>Melinis</i>	<i>Urochloa</i>	
	<i>Cymbopogon</i>	<i>Microchloa</i>		
	<i>Cynodon</i>	<i>Monocymbium</i>		
	<i>Dactyloctenium</i>	<i>Oxyrhachis</i>		
	<i>Dichanthium</i>	<i>Panicum</i>		
	<i>Digitaria</i>	<i>Paratheria</i>		
	<i>Dinebra</i>	<i>Paspalidium</i>		
	<i>Diplachne*</i>	<i>Paspalum</i>		
	<i>Echinochloa</i>	<i>Pennisetum</i>		
	<i>Eleusine</i>	<i>Perotis</i>		
	<i>Elionurus</i>	<i>Pogonarthria</i>		
	<i>Enneapogon</i>	<i>Rhytachne</i>		
	<i>Enteropogon</i>	<i>Rottboellia</i>		
	<i>Eragrostis</i>	<i>Schizachyrium</i>		