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The deforestation story: testing for anthropogenic origins of Africa's flammable grassy biomes

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Africa has the most extensive C4 grassy biomes of any continent. They are highly flammable accounting for greater than 70% of the world's burnt area. Much of Africa's savannas and grasslands occur in climates warm enough and wet enough to support closed forests. The combination of open grassy systems and the frequent fires they support have long been interpreted as anthropogenic artefacts caused by humans igniting frequent fires. True grasslands, it was believed, would be restricted to climates too dry or too cold to support closed woody vegetation. The idea that higher-rainfall savannas are anthropogenic and that fires are of human origin has led to initiatives to 'reforest' Africa's open grassy systems paid for by carbon credits under the assumption that the net effect of converting these system to forests would sequester carbon, reduce greenhouse gases and mitigate global warming. This paper reviews evidence for the antiquity of African grassy ecosystems and for the fires that they sustain. Africa's grassy biomes and the fires that maintain them are ancient and there is no support for the idea that humans caused large-scale deforestation. Indicators of old-growth grasslands are described. These can help distinguish secondary grasslands suitable for reforestation from ancient grasslands that should not be afforested.

This article is part of the themed issue 'The interaction of fire and mankind'.

1. Introduction

Africa supports the largest extent of grassy biomes dominated by C4 grasses in the world [1]. They cover some 70% of the continent and are the dominant vegetation between latitudes 30° south and north of the equator. Savanna, defined as having a discontinuous layer of trees and shrubs with C4 grasses prominent in the herbaceous layer, is by far the most extensive biome. The grassland biome, also with C4 grasses in the herbaceous layer but with no trees, occurs in uplands such as the highveld of South Africa and in floodplains and on other soils hostile to trees. C4 grasses can be highly productive in the rainy season but dry out becoming highly flammable in the dry season. Africa's grassy biomes accounted for greater than 70% of global burnt area from 1997 to 2009 [2].

African grassy biomes occur across a wide rainfall gradient (200–2000 mm MAP) [3]. In this respect, they contrast with the distribution of grassy biomes in Europe which generally occur in drier or cold climates. Africa's grassy biomes form 'mosaics' with forests, defined here as closed woody formations lacking a C4 grassy understory. The juxtaposition of low-biomass open ecosystems with high-biomass closed forests has long puzzled ecologists. Because competition for light is asymmetric, tall plants should displace shorter plants so that, given sufficient time, forest should develop where the climate is suitable for tree growth. C4 grasses, with few exceptions, are intolerant of shade, so their presence in a woodland understory is an anomaly for the successional concept. The anomaly is generally explained in European forests by disturbances,

typically human deforestation, and grasslands are considered successional to forests [4]. By the same reasoning, tropical and subtropical forest/grassland mosaics in Africa were also thought to be the products of deforestation [5,6].

2. Explanations for the extent of Africa's grasslands

The idea that climate determines the distribution of savanna and associated grassy biomes was first challenged by Whittaker [7], who identified a climate zone on his temperature–precipitation plane where vegetation structure was not predictable. Grasslands, savannas, shrublands, woodlands and forests all occur in this climate zone. Bond [8] labelled this climate zone ‘ecosystems uncertain’. Its global extent is vast and covers most of Africa's savannas. The extent of the mismatch between climates and potential forest vegetation has since been explored by physiologically based dynamic global vegetation models (DGVMs), analyses of satellite imagery, ground vegetation maps and published studies on tree biomass [9–12]. All these studies, using different approaches, recognize that large areas of Africa's grassy biomes occur where the climate can support forests. The causes of this continental-scale mismatch between actual and potential vegetation has, however, been interpreted very differently. A developing school of thought is that the grassy biomes and forests represent alternative states [10,11]. Both grassland and forest systems would be ancient, maintained by positive feedbacks promoting long-term stability of each state. In this view, fire has been considered the key process maintaining savannas in seasonally humid climates suitable for forests [13]. Forests resist fires by shading out grassy fuels and altering the microclimate. The areal extent of forests versus savannas should wax and wane depending on circumstances favouring the fire feedback or, from a forest perspective, the ability of forest margins to recover rapidly from fire and colonize adjacent grasslands [14,15].

The more traditional view is that forest/grassland mosaics are the product of widespread deforestation. This hypothesis, generally held in the tropics, is at least a century old. It typically assumes that fires are ‘unnatural’ in that they are ignited by people and that these anthropogenic fires have caused major deforestation [5,16]. This view has dominated public opinion and underpinned projects funded by development agencies, national legislation restricting the use of fire and proposals for afforestation of grassy systems. Recently, it has been the implicit or explicit motivation for large-scale afforestation to sequester carbon to reduce greenhouse gases (e.g. [17,18]). Large discrepancies between potential and actual woody biomass are taken as indicators of preferred sites for ‘reforestation’ for carbon sequestration [19]. The most extreme example of this view is expressed in a global map of reforestation potential produced by the World Resources Institute (WRI) [20]. The global map is based on identifying areas with a large difference between actual and climate-potential vegetation [21]. The map is being used as the basis for an ambitious reforestation programme, the Bonn Challenge, which aims to restore 1.5 million km² of ‘degraded’ land by 2020. Vast areas of Africa's high rainfall grasslands and savannas have been mapped as suitable for reforestation (figure 1). While there is good evidence for extensive deforestation in South America and parts of southeast Asia [23,24], it is far from clear that this is

Figure 1. Potential reforestation areas in Africa according to the *Atlas of Forest Landscape Restoration Opportunities* (WRI [20]). Dark purple areas indicate grassy biomes, orange areas are grassy biomes considered opportunities for mosaic and ‘wide-scale’ restoration. Light purple areas are areas unsuitable for reforestation because they already support closed forest or are too arid for tree planting. Adapted from [22].

also the case in Africa [24–28], especially at the scale mapped by the WRI [22].

Here we consider the implicit assumptions of plans to reforest Africa by reviewing: (i) evidence for the antiquity of savannas, (ii) the antiquity of fires in grassy biomes, and (iii) the biodiversity and successional responses of the grassland biota to afforestation and deforestation. As Africa is famous for its surviving megafauna, we also briefly consider mammal herbivory and fire/herbivore interactions in maintaining non-forested ecosystems.

3. The antiquity of savannas

If savannas are the products of anthropogenic deforestation, then these supposed ‘early successional’ systems would be of recent origin, perhaps, in the order of a few millennia in ancient densely settled areas. Diverse studies indicate that the flora and fauna is far older. C4 grasses appeared in the Oligocene, some 30 Ma [29]. However, their assembly and rapid spread as a savanna biome occurred more than 20 Myr later in the Late Miocene (approx. 8 Ma) [30]. Evidence for their spread comes from carbon isotopes, which are markedly divergent in plants with ancestral C3 versus C4 photosynthetic pathways. Plant material with C3 and C4 isotope signals are preserved in the bones and teeth of animals and in fossil soils. Fossil evidence indicates that the savanna biome first appeared in the tropics, spreading from there to higher latitudes [30,31]. The retreat of forests and their replacement by savannas has been attributed to Late Miocene aridity or an increase in fire activity. There is clear evidence that aridity was a major factor in forest retreat in Eurasia and North America based on numerous pollen records (e.g. [32]) and analyses of phytoliths, the silica bodies in plant cuticles [33]. In Africa, the best fossil records are from areas that today are arid [31]. Humid regions, where grass-fuelled fire would have been common, are generally deeply weathered and lack ancient fossil deposits so that there is a taphonomic bias against terrestrial fossil evidence

Figure 2. Boxplots showing $\delta^{13}\text{C}$ isotope signals (parts per mil) down soil profiles in an open/closed vegetation mosaic in northeastern South Africa. The left figure indicates closed thicket/savanna and the right figure forest/grassland comparisons. Soil depth is a surrogate for age of the soil carbon. Convergence of the signal at depth indicates that the thicket and forest have colonized ancient grasslands. Adapted from [51].

for fire as an agent rolling back forests. However, the role of fire in the spread of African savannas can be traced from fossil charcoal, especially from marine cores. These show a sharp increase in charcoal fluxes also from the Late Miocene [34,35]. Increased fire activity within the last approximately 10 Myr, is a worldwide phenomenon with evidence for a surge in charcoal fluxes in the North Pacific, the North and South Atlantic off Africa, and terrestrial records in Australia [36]. In Africa, dated molecular phylogenies indicate that growth forms characteristic of fire-maintained savannas developed at least 6–8 Ma in the tropics spreading to South Africa by 1–2 Ma [37]. Both fossil and phylogenetic evidences of the radiation of the bovids, the lineage of antelopes characteristic of contemporary African savannas, show a rapid proliferation of grazing mammals from the Pliocene [38–40]. Both fossil and phylogenetic evidences, therefore, indicate that grassy biomes and the fires that maintain them are not merely anthropogenic phenomena. They preceded human control of fire by millions of years. Humans adopted an ancient ecological process for their own uses. Africa was last forested more than 10 Ma. Fires occurred long before humans and were a major factor in their replacement by C4 grassy systems according to simulations of Late Miocene conditions [41].

By the Pleistocene (2.6 Ma), savannas covered extensive areas of Africa. In the Late Pleistocene, during the cool period from approximately 110 000 to approximately 12 000 years BP (the last glacial), pollen and alkane evidence from marine cores off West Africa show that the Congo forests had retreated to a tiny enclave [42–44]. This retreat is part of a more general trend of a retreat of tropical forests in the Last Glacial Maximum [45]. The extent of this retreat cannot be explained by the cooler, drier climates alone. DGVM modelling indicates that low CO_2 , which favours C4 grasses but inhibits tree growth, was a major contributor [45–47]. Thus, in the 2.6 Myr of the Pleistocene, grassy biomes would have been the most extensive vegetation cover of Africa, the ‘norm’ for the continent, not forests. A million-year record of charcoal from a marine core off West Africa indicates these grasslands were burning [48].

As climates became warmer and CO_2 increased in the Holocene (approx. 12 ka), forests began to spread, colonizing the ancient grasslands. In several intensely studied sites in East Africa, for example, areas that are currently forests were flammable grasslands in the last glacial as indicated by charcoal cuticles signifying frequent fires [49]. In South

Africa, carbon isotope analyses revealed that grasslands and savannas, long interpreted as the products of Iron Age deforestation over the last two millennia, were ancient [50] (figure 2). C14 dating indicates that the forest colonized the grassy biomes probably in the last two or three millennia [52]. In an interesting modelling exercise, Moncrieff *et al.* [53] explored the effects of initial conditions at the end of the last glacial (along with climate, CO_2 and fire) on the modern distribution of savannas versus forests in Africa. Their DGVM simulations showed that contemporary distribution of savanna and forest was best explained if Africa emerged from the last glacial period as a grass-dominated continent. Strikingly different forest distribution was simulated if forests were assumed to dominate Early Holocene vegetation. Thus, at the start of the Holocene, with warmer wetter high CO_2 conditions, and human populations beginning to expand, the ancient vegetation of Africa was dominated by grasslands, not forests.

Turning towards the historical period, the evidence for deforestation in Africa is also ambiguous. Fairhead & Leach [24–26] considered that the idea of extensive deforestation in West Africa was a cultural construct with little empirical support. They pointed out that deforestation statistics for West Africa depended critically on the definition of ‘forest’. Changing definitions through time, they argued, explain the apparently alarming deforestation in several West African countries. The problem of defining forest is a general one in tropical landscapes [54–56]. Ratnam *et al.* [57] provided a functional definition for distinguishing forest from ‘savanna’ based not on the trees but on the presence of a highly flammable, shade-intolerant C4 grassy understory in savannas and its absence in forests. It is the presence of the grasses that is informative as to the feedbacks that maintain the system and not merely the biomass and basal area of trees. Fairhead & Leach [25] drew on historical records in Guinea for information on forests versus savannas in the nineteenth century. Contrary to the general perception that forests had declined under growing populations, they showed that forests had expanded not contracted during the twentieth century. For example, Ziama forest reserve in Guinea, a large forest patch set aside for conservation and a world Heritage site, had been a savanna according to accounts from the nineteenth century [27]!

With increasing availability of satellite imagery, studies of deforestation, reforestation and afforestation [58] in Africa are

allowing much greater accuracy in monitoring landcover changes. As remote sensing techniques improve, there will be progressively more accurate estimates of forest carbon loss. Unfortunately, these studies seldom provide any historical context to the analyses of change. As Fairhead & Leach's [25–27] analyses for West Africa show, the historical origin of a forest may be as recent as the nineteenth century. Their analysis implies that forest patches formed part of an anthropogenic landscape in some regions, created by human activity and removed by human activity. Over the longer term, satellite imagery will allow us to track the changing landcover of Africa, and the changing use of fire, to a level of accuracy unimagined previously.

4. Grass-fuelled fire regimes

African savanna fire regimes are driven by grassy fuels. They differ strikingly from woody fuels characteristic of much of the Northern Hemisphere such as conifer woodlands and Mediterranean shrublands or the eucalyptus forests of southern and eastern Australia [59,60]. In these woody ecosystems, fuel continuity during large fires is coincident with hot dry conditions. In savanna fires, by contrast, fuel continuity depends on high rainfall promoting grass growth. Thus, high fire activity in Africa is associated with high rainfall or, in arid areas, sequences of wet years when grassy fuels accumulate [61,62]. Fuel continuity in savannas can be broken by heavy grazing and by high tree cover suppressing grass biomass. For example, Archibald *et al.* [62] showed that fire activity detected from satellites declined abruptly when tree cover exceeded 40%. Typically, savanna fires are extinguished within a few meters of closed-forest margins. Both the lack of grassy fuels and the forest shade, and changes in the microclimate, especially a reduction in wind speed, have been identified as causes of forest resistance to burning [63]. Nevertheless, under extreme conditions (high wind speeds, high temperatures, low humidity, high grassy fuel loads) fires originating in savannas can penetrate deep into closed woody vegetation [64].

The intensity of fire, and therefore, the impact on trees, varies with fire season. In general, low-intensity fires occur early in the dry season when grasses are not yet fully cured. High-intensity fires are typical of the late dry season particularly just before the rainy season starts. Long-term fire experiments have shown that early-season burns allow a much broader range of fire-resistant and fire-sensitive trees to occupy a savanna [9,65–67]. By contrast, late-season burns are much more damaging to trees, and only the most fire-resistant species survive frequent late-season burns. Thus, changes in the timing of fire can significantly influence tree cover in savannas and, presumably, the damage caused by fire burning into forest margins.

5. How might humans have influenced savanna fire regimes?

Archibald *et al.* [68], in a seminal paper, analysed human impacts on fire regimes by identifying six distinct stages in hominin mastery of fire and simulating the effects of these on the fire regime. From (i) an initial lightning-dominated fire regime, (ii) humans began to make use of lightning

fires, (iii) learnt to ignite fires without lightning, (iv) increased ignition frequency as populations expanded, (v) developed agropastoralism, reducing fuel continuity, and (vi) began the modern period with rapid population expansion and intensification of impacts.

They found that savanna fires in Africa are relatively insensitive to ignition frequency. A single ignition, whether from lightning or a match, can produce a fire that burns for days in extensive open savannas. However, humans can have large effects on grass-fuelled fire regimes by changing the timing of fires (stage 3). Lightning ignitions are most common in the transition from the dry to the wet rainy season so that 'natural' fires would have been late dry season fires. By contrast, human ignitions are concentrated in the early to mid dry season, when fires are more easily controlled. Studies of contemporary burning practices in West Africa show that people burn as soon as the curing of grasses permits, when fires are least likely to burn out of control [69,70]. Thus, one of the clearest human effects on fire regimes would have been a switch from high-intensity late dry-season fires to low-intensity early dry-season fires. The latter, as noted above, favour fire-sensitive trees and are least damaging to forest margins.

The effects of humans on fire regimes can be seen at continental scale. Archibald *et al.* [71] used remote sensing to classify savanna fires as frequent and either large and intense or small and of low intensity. They note that the sparsely populated savannas of Northern Australia are characterized by frequent large fires, whereas densely populated areas of African savannas, are characterized by frequent small fires of low intensity. From what we know from long-term burning experiments in both continents, the small, frequent, 'cool' fire regime of densely settled parts of Africa would be the least damaging to trees, and therefore, least likely to be a major cause of deforestation. Their global analysis is consistent with regional studies of fire regimes in West Africa where 'humanized' fire regimes produce small, frequent, cool fires that help protect fields, homes and, indeed, forest patches [25,69,70].

In summary, human impacts on fire regimes in Africa are unlikely to have increased fire damage to forests once people learned to burn at will. The scale of areas affected by human-altered fire regimes would probably be small, with the largest effects perhaps restricted to hilly country, where targeted ignitions in flammable grassy fuels would have been most likely to increase fire frequencies. Current burning practices are designed to reduce damage to crops, property and forest patches. Indeed, Archibald *et al.* [68] conclude that the largest human impacts on fire regime, prior to high human settlement in the last century, would have been a *reduction* in burnt area when pastoralism became common (stage 5 in human fire use). Heavy grazing by livestock reduces fuel loads and fuel continuity sufficiently to create barriers to fire spread.

6. Herbivory and grassy biomes

The role of the African megafauna in shaping large-scale vegetation patterns today or in the past is far from resolved. African savannas occur in two major types, small-leaved savannas dominated by Mimosaceae and large-leaved savannas dominated by Caesalpiniaceae and Combretaceae [72]. The former occur in drier climates and/or on fertile soils.

The latter occur in more mesic climates and typically on leached nutrient-poor soils. The African megafauna is most diverse and abundant in thorny (Mimosaceae-dominated) savannas [73–75]. However, forests are most likely to occur in the higher-rainfall savannas [10,11] where fire is typically the major consumer [62]. Given our focus on deforestation as an explanation for the existence of the grassy biomes, we focus on fire as the major ecological and selective process in the wetter savannas of Africa. We acknowledge that this is an oversimplification, especially, perhaps, as regards elephant/fire interactions at forest margins.

7. The nature of ancient grasslands

Though Africa's grasslands are ancient, clearly deforestation has occurred in places and secondary grasslands have replaced them. Reforestation projects have been important for restoring key ecosystem services that forests can supply. Is it possible to map 'old-growth' grassy biomes as distinct from secondary grasslands so as to help guide reforestation plans? And if so, at what scale?

(a) Diversity and endemism

Given the antiquity of C4 grassy ecosystems in Africa, one would expect natural systems to have a diversity of species endemic to these open grassy habitats. Bond *et al.* [76] explored the question of whether Madagascan grasslands are ancient or, as has long been argued, products of deforestation in the 2000–4500 years since people settled the island. They argued that if the grasslands were secondary they would be expected to have low diversity, few if any open-habitat specialists, and low species turnover across environmental gradients. They showed that this was not the case and argued that Madagascan grasslands have ancient origins. A recent study based on new collections has shown that 40% of Madagascar's grasses are endemic, supporting the argument of ancient origins for open vegetation on the island [77]. Furthermore, different centres of grass endemism were identified, indicating that grasslands were widespread across the island before settlement.

It is surprising that the question of the origin of grassland habitat endemics has not been more widely used to evaluate the deforestation hypothesis. An interesting contrast between ancient and 'new' grassy systems has been noted for North America. The tall grass prairies of the eastern Great Plains are maintained by fire and can be replaced by forests with fire suppression [78]. Anderson [79] has argued that these prairies are the products of anthropogenic burning (see also [80]). Anderson argued that the biota is not endemic to the grasslands but cobbled together from adjacent broad-leaved forests or arid western biomes. Patterns of diversity and endemism are quite different in the grassy biomes of the southeastern USA. Noss [81] argues for an ancient origin of these grasslands. They are also largely fire-maintained and have been transformed over large areas into broad-leaved deciduous forests following fire suppression after European settlement. The southern grasslands, unlike prairies, experienced a warm climate in the last glacial. The plant life is rich and diverse accounting for nearly one-third of the North American flora. Nearly 1000 species are endemic to grassland habitats in comparison to less than 100 in Great Plains grasslands. The southern grasslands also support a rich endemic fauna restricted to open habitats. As for African

grassy systems, these fire-dependent savannas have long been assumed to be the products of anthropogenic burning by Native Americans. But the rich endemic flora and fauna indicate much more ancient origins [81].

In South Africa, the grassland biome is rich in plant species with many endemics [82,83]. The grasslands of the eastern high-rainfall parts of the country were interpreted, as elsewhere in the world, as products of deforestation following the arrival of Iron Age farmers in the region some 2000 years ago [6]. Their high diversity indicates a much older origin, consistent with pollen records of grasslands present long before crop farming [28] and carbon isotope analyses indicating that forests colonized grasslands [50,52]. The grassland fauna is also diverse with the distribution of 10 of South Africa's globally threatened bird species centred in the grassland biome [83]. The grasslands have been extensively forested with pines and eucalyptus, justified from a conservation perspective by their supposed anthropogenic origins. Grasslands such as these have become prime targets for 'reforestation' motivated increasingly by carbon sequestration to reduce greenhouse gas emissions [18].

(b) Plant traits

Plant traits can reveal whether trees, shrubs and forbs in grassy systems are remnants of catastrophic deforestation or a normal component of frequently burnt savannas. For example, Ratnam *et al.* [57] proposed a suite of traits that would help distinguish fire-maintained savanna woodlands from fire-sensitive closed forests. These include, for trees, thicker bark, the presence of insulated buds (allowing post-burn resprouting), branch architecture (growing wide versus growing tall), more open canopies with lower leaf area, large underground storage in saplings and vegetative propagation through clonal spread.

(c) Underground trees

One of the most extreme woody plant responses to frequent savanna fires is development of dwarfism and reproductive maturity within the flame zone. 'Underground' trees (geoxylic suffrutices) are common in frequently burnt savannas, growing in environments with slow woody growth rates [37,84]. Underground trees are taxonomically diverse but, by definition, have tall-tree relatives in forests or savannas [84]. They are common in central and southern African high rainfall savannas but, according to White [84], they are absent from West Africa. This growth form is also common in South American savannas in unrelated lineages indicating convergent responses to grass-fuelled fire regimes [85,86]. Underground trees are thought to be slow growing so that their presence indicates an ancient grassland system. Their life history and ecology is poorly studied in Africa but they do provide tracers of the ancient origins of fire-maintained African savannas [37].

(d) Forbs

The ecology of forbs (non-graminoid herbs) has been neglected until recently. Understandably, research on African grassy biomes has focused on their utility as food for grazing animals. However, forbs are emerging as key indicators of ancient grasslands [87]. In South Africa, there are marked changes in forb life histories along climate/altitudinal gradients

Figure 3. The distribution of long-lived perennial forbs in grasslands along a precipitation gradient, eastern South Africa. Number of species in 1000 m² plots relative to mean values are shown.

(figure 3). Annuals and short-lived perennials are common in more arid grassy systems. However, in higher-rainfall regions, short-lived forbs are extremely rare or absent. Instead, the forb flora is dominated by long-lived perennial plants with large underground storage organs (USOs). Many of these forbs have fire-stimulated flowering with large numbers of plants flowering in the first growing season after a burn [88]. Forbs with USOs have been implicated as key savanna resources for early hominins providing a food source over the long dry seasons to replace the food resources of forests [89]. The distribution and ecology of plants with USOs is poorly known within African tropical and subtropical grassy systems and, indeed, is poorly studied elsewhere in warm climates too. Similar growth forms have been reported for the southern grassland biome of Brazil [90] and South American savannas (cerrado) [91]. The presence of forbs with large USOs is emerging as an important indicator of ancient grasslands [87].

8. Responses of grassland biota to afforestation, disturbance and deforestation

The responses of fire-adapted grassland plants to afforestation can help indicate the resilience of these ecosystems to forest expansion and contraction. Many highly persistent plants are poor colonizers [87,92]. The trade-off between persistence and colonizing ability predicts that forbs with USOs that are highly persistent, may be poor colonizers of secondary grasslands created by deforestation. Recent studies in South African grasslands and savannas have explored the dynamics of the forb component in relation to afforestation, deforestation and cultivation [93,94]. If grasslands are secondary products of deforestation then the grassland biota should be weighted towards rapidly colonizing species and recovery from land-cover change should also be rapid, at least relative to forests. However, this was not the case for mesic South African grassy systems with a large component of persistent forbs with large USOs (figure 3). The forb flora is very intolerant of shade. Suppression of fires, resulting in accumulation of undecomposed grass litter, caused eradication of this forb layer after approximately 10 years of fire suppression [95]. This response is in marked contrast with forbs in North American tall-grass prairies. Here forb diversity

Figure 4. Comparison of changes in number of species with time in secondary forests versus forbs in secondary grasslands in coastal dunes, eastern South Africa. The horizontal line indicates mean species richness in old-growth grasslands. Data from [93].

declined with increased frequency of fire and the highest diversity was in unburnt, but grazed prairies [96]. These strikingly different responses of the ancient humid grasslands of South Africa versus the new post-glacial Great Plains grasslands of North America point to the need for caution in generalizing ecological results and the need for more studies in ecologically diverse settings.

The extreme intolerance of shade in grassland forbs in South Africa is also apparent from afforestation studies. Parr *et al.* [97] compared both plant and insect diversities in savannas invaded by ‘thicket’, a closed woody formation, in a South African national park. In their study, thicket invasion caused large turnover of plant species, especially forbs, with similar large turnover in ant species. Large losses of plant species, again especially among forbs, has been observed following the establishment of conifer plantations and their subsequent removal [93,94] (figure 4). Secondary grasslands established rapidly, though with entirely different dominant grass species. The forb component was dominated by weedy species not present in the undisturbed grassland. Neither forb diversity, nor the original forb composition, had recovered decades (20–40 years) after removal of the conifers (figure 4). Over the same period, and on coastal dune sites, restored forests showed a linear increase in species richness of plants with time, in striking contrast with the complete lack of such a trend in the grasslands (figure 4) [93]. Thus, forest appears to be far easier to restore in this system than grasslands, at least by natural successional processes.

9. Conclusion

African grassy biomes are ancient and were even more extensive in the Pleistocene when human populations were sparse. Their coexistence with forests is best explained as the result of positive feedbacks of each biome type on processes that maintain each state. Fire is the critical feedback in humid C4 grass-dominated savannas, and suppressed by closed forests. Fire is an ancient process, long preceding the emergence of fire as a tool used by hominins. Forests expanded in the

Holocene in Africa despite increasing human populations and, presumably, more intense use of fire. The common assumption of widespread deforestation in Africa, fuelled by anthropogenic fires, is not supported by palaeoecological evidence. Subcontinental-scale reforestation plans are at variance with current knowledge of the antiquity of the grassy systems. These are not reforestation plans but afforestation on a massive scale. The repercussions of geoengineering on this scale are far from clear, whether for local economies or for the stated benefit of reducing global warming by carbon sequestration [22]. A more explicit accounting of the costs and benefits, both local and global, is essential before embarking on large-scale afforestation projects. Where afforestation (or reforestation) is beneficial, we are beginning to develop

pointers as to how to identify ancient versus secondary grasslands so as to guide the location of restoration efforts.

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