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Commentary: The role of palaeoecology in reconciling biodiversity conservation, livelihoods, and carbon storage in Madagascar

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A Commentary on

[The role of palaeoecology in reconciling biodiversity conservation, livelihoods and carbon storage in Madagascar](#)

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Introduction

Currently, 80% of Madagascar is treeless grassland. Identifying lost savanna woodland and grassland, forest, and heathland before pastoralism was introduced *circa* 0.5–1 ka (Hixon et al., 2021) informs conservation planning/restoration on the island. Gillson et al. (2023; hereafter G2023) warn that binary classification of “*all savannas and heathlands as degraded forests is ecologically inaccurate*”, setting a “*false dichotomy between forest-grassland*”, and “*has diverted attention away from the loss and conversion of heathlands and savannas.*”

We agree, and were surprised to see these statements (italicised) attributed to us (Joseph and Seymour, 2020, 2021; henceforth J&S20,21), two years after we debunked outdated “*forest-grassland*” dichotomies for Madagascar’s Central Highlands (MCH). We concluded: “*This interdisciplinary review challenges the century-old extreme perspectives ... Evidence supports neither (1) a forested MCH with secondary grasslands ... nor (2) MCH characterised by vast natural treeless grassland ... Findings support a more wooded, more ericoid-rich past, with grasses coexisting with trees as woodland understory and as components of ericoid systems. At fine scales, a complex mosaic ... seems likely, including smaller treeless grasslands.*” We postulated an eight-habitat mosaic (not two), with savanna >30%, and 10-fold more heathland than today (Joseph et al., 2021). We clearly (1) opposed and disproved the dichotomy, and (2) have never found “*all savannas and heathlands*” to be degraded forest.

Trees/grass/savannas and fire

Savanna biomes are characterised by a continuous C_4 grass layer, ranging from grass-dominated systems to tree-dense savanna woodland. Although both are savanna, woodland is functionally distinct from treeless grassland. Annually, >100,000 km² of MCH grassland burns anomalously relative to comparable ecoregions globally (Joseph et al., 2023). Most (95%–99%) fires are human-lit, and most severe where human densities are lowest (Kull, 2003). Globally, savanna tree-cover >45% limits fire, but tree-cutting/frequent fires convert woodland (Trapnell, 1959) and heathland (Gil-Romera et al., 2019) to fire-adapted grassland lacking trees, which can expand into regions where climate supports forest (Staver et al., 2011).

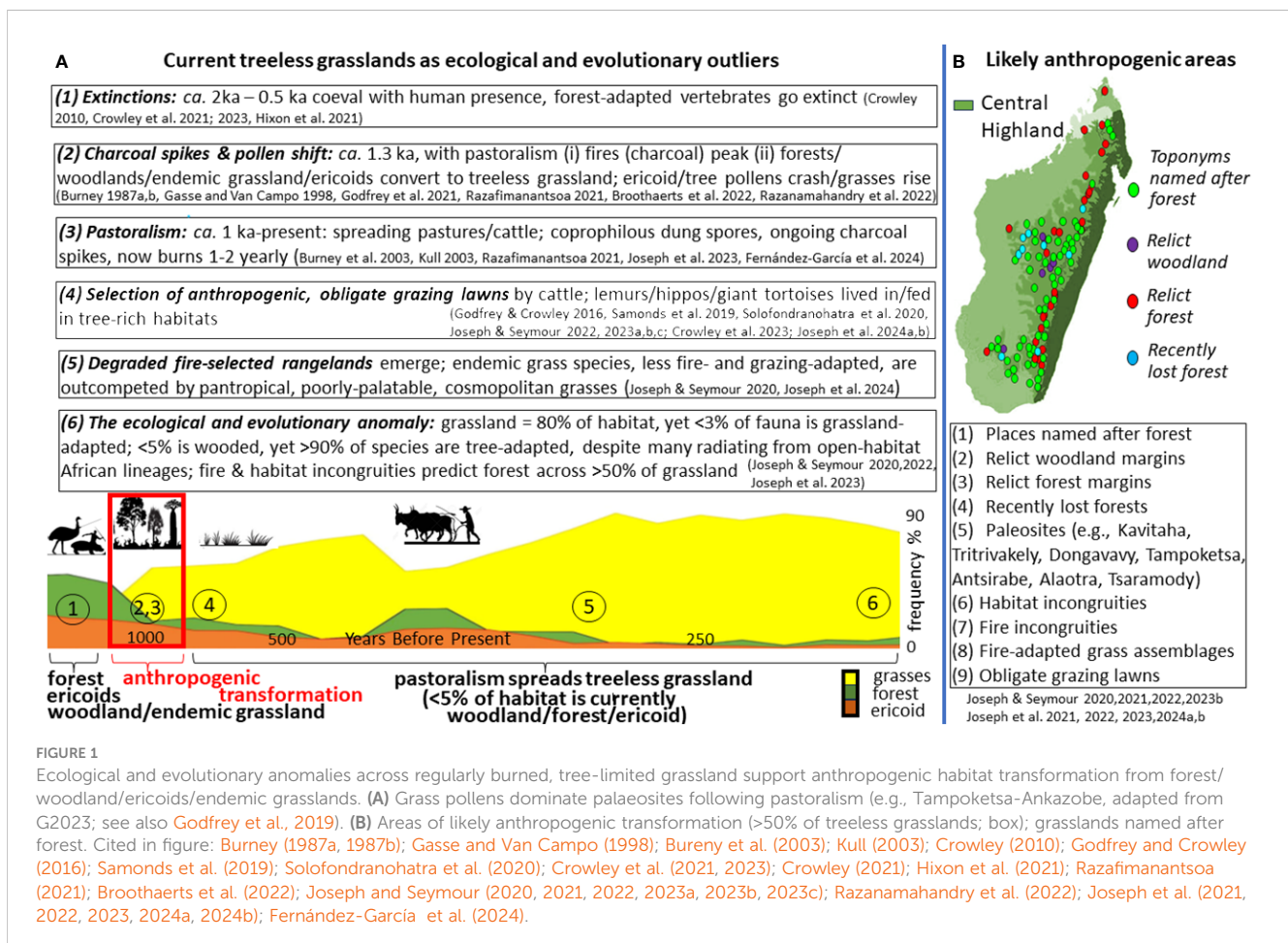
Wakeling et al. (2015), citing Bond et al. (2008), specified Madagascar's "treeless grassland" as systems where "trees are absent", and despite annual human-lit fires (Kull, 2003), consider them ancient, non-anthropogenic systems, formed before human settlement. This view proposes woodland as naturally <5% (Solofondranohatra et al., 2018); with grassland-limited fauna supporting their antiquity (Bond et al., 2008); that human-lit fires and cattle are surrogates for natural fires/endemic grazers, and that obligate grazing lawns coevolved with extinct C_4 -feeding giant tortoises and "pure" C_4 -grazing hippos (Bond et al., 2008; Solofondranohatra et al., 2020). We provide an alternative: Figure 1

details evidence for humans extirpating tree-adapted, forest-feeding megafauna that were never pure C_4 -feeders, transforming (by cutting/burning) a mosaic of larger woodlands/forests/ericoids and smaller grasslands *circa* 1 ka, to derived treeless grassland, maintained by introduced cattle and human-lit fire, where fire-adapted cosmopolitan grasses outcompete endemic grasses.

Woodlands are savannas; ericoid-habitats are heathlands

Woodlands, with their C_4 -grass layer fall within the savanna biome. They are distinct from forest (closed-canopy biomes, where shade limits C_4 -grasses). For G2023 to ascribe (1) a binary "forest-grassland" dichotomy, and (2) "all savannas and heathlands" being "degraded forests" to J&S20,21, requires two errors.

The first is conflating woodland (savanna) and forest, creating an ecologically irrational dichotomy (woodland/forest vs. grassland). This is strange, because G2023 understand woodland as savanna, stating: "Tapia ... woodlands are now classified as savannas". They also clearly regard savannas and forests as separate categories ("savannas and heathlands as degraded forests is ... inaccurate"). J&S20 unambiguously describe savanna: "there is no debating the ancient existence of grassy woodland, nor of grassy patches vacillating in size with prevailing fire and climate



conditions". J&S20 define "open canopy" Tapia with C₄-grass understories as akin to Miombo (savanna woodland), but distinct from closed-canopy forest. Similarly, J&S21 emphasise "forest-limited endemic fauna support anthropogenic transformation from woodland". If tree-rich savanna woodland had not been anthropogenically transformed, aspects of today's grasslands would likely have harboured tree-adapted fauna, which are now limited to forest. Equally strange is G2023's missing our nine vegetation studies, citing instead papers documenting faunal radiation (J&S20,21 find >90% of species are adapted to tree-rich habitat; <3% are grassland-limited).

The second error is disregarding our reference to ericoids. J&S20,21 describe transformation of grassy woodlands/smaller grasslands/forests/ericoids to treeless grassland; J&S21 details pre-human heathland presence, noting "even today these areas harbour ericoids". J&S20,21 are not ecologically inaccurate: woodlands with C₄-grass understories are savannas; ericoid habitats are heathlands.

Preserving ecological accuracy

Where disturbance incongruities exist, re-evaluation is needed (Lehmann et al., 2011), because incongruities suggest anthropogenic transformation (Thompson et al., 2021; Joseph et al., 2022). G2023 assert J&S20,21 miss "a key challenge for an informed and bottom up approach to conservation and restoration, which is to distinguish which open landscapes are ancient or anthropogenic, their historic nature and their current value to communities in ecosystem service provision". Yet our findings (1) report nine ways of identifying regions/sites likely degraded by anthropogenic impacts (involving >50% of grasslands; Figure 1A); (2) promote indigenous knowledge/history (much grassland is named after forest; Figure 1B), and (3) highlight anthropogenic, island-wide ecosystem breakdown.

Regarding ecosystem services: ongoing tree-removal/fire-setting initiated >1 ka causes nutrient-rich soil loss (Brosens, 2022), silting lakes, lowering water quality (Bakoariniaina et al., 2006), and reducing marine and terrestrial diversity (Raharimahefa and Kusky, 2010). These degrade rangelands/grasslands/forests and threaten livelihoods (Styger et al., 2007; Neugarten et al., 2016; Joseph et al., 2023). Despite foreign, paternalistic promotion of burning practices, many pastoralists are aware that this exacerbates landscape degradation/poverty/armed conflict/gender inequality

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(malnutrition is pervasive; UNICEF, 2021) and strive for economic diversification (Joseph et al., 2024b).

Conclusions

The binary classification/ecological inaccuracy raised by G2023 is not held by mainstream researchers, who support pre-settlement habitat mosaics (Joseph et al., 2021; Lehmann et al., 2022; Crowley et al., 2023). The "key challenge" of identifying anthropogenically-impacted areas, and their value/risk to people, is not "missing" (G2023), but well underway. Conservation lacks resources: framing research around already-resolved debates (there is no dichotomy) and mis-citations undermines transdisciplinary cooperation and introduces unnecessary distractions.

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GJ: Conceptualization, Writing – original draft, Writing – review & editing. CS: Conceptualization, Writing – original draft, Writing – review & editing.

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