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

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A Commentary on

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By Joseph GS and Seymour CL (2024). *Front. Conserv. Sci.* 5:1389498. doi: 10.3389/fcosc.2024.1389498

We welcome Seymour and Joseph's commentary, which acknowledges the complexity of Malagasy landscapes (Joseph and Seymour, 2024). The multiple landscape elements that are present throughout most of the island provide a wealth of biodiversity habitats and ecosystem services (Bond et al., 2023; Silander et al., 2024). The climatic gradient from wettest in the northeast to the dry south west, as well as the interacting effects of fire and topography, means that only the northeast contains true forest, in the sense of a closed or near-continuous canopy (Straka, 1996; Moat and Smith, 2007). The rest of the island comprises a mosaic of dry forest, open woodland, savanna, ericoid heathland, and grassland, with tree cover varying from 0% to 75%, and patches of closed forest, largely confined to ravines and riverine areas (Robinson et al., 2021; Silander et al., 2024). The distinction between these vegetation types is important since they house different (though sometimes overlapping) suites of biodiversity. Palaeoecological work has shown the existence of these open, grassy, and mosaic ecosystems, as well as the presence of fire, long before human arrival in Madagascar (Burney, 1987; Gasse and Van Campo, 2001; Bond et al., 2008; Virah-Sawmy et al., 2009b; Vorontsova et al., 2016; Hackel et al., 2018; Vorontsova et al., 2020; Razafimanantsoa, 2022).

While some open grasslands have been derived from anthropogenic clearing and burning, others are ancient and rich in endemic species (Bond et al., 2019; Vetter, 2020;

García-Dory et al., 2021; Lehmann et al., 2021). Understanding the landscape history and how it evolved with changing land use and environment is critical in planning appropriate restoration and management. The assumption that open and mosaic landscapes are degraded forests is still a dominant narrative in Madagascar and has left them vulnerable to afforestation using exotic species such as pine and Eucalyptus (Carriere and Randriambanona, 2007; Charles and Dukes, 2008; Stickler et al., 2009; Bond, 2019; Kull et al., 2019; Randriambanona et al., 2019). Despite growing awareness of the complexity of landscape mosaics, deforestation rates in Madagascar are still frequently measured relative to the erroneous baseline of 100% forest cover (Huff and Orenge, 2020; Gillson et al., 2023), or in other cases based on an overestimation of original forest cover (McConnell and Kull, 2014; Amelot, 2017). In the twentieth century, the binary categorization of forest versus all other vegetation types as “non forest” led to inflated estimates of tree cover losses. The combination of inflated forest loss and underlying assumptions regarding degradation in turn impacted communities who were then blamed for landscape mismanagement (Virah-Sawmy and Ebeling, 2010). We give some examples of the effects of these misunderstandings in Gillson et al. (2023).

Joseph and Seymour (2020, 2021) (hereafter J&S) set out to investigate the longevity of open grasslands in the Highlands of Madagascar, as proposed by Bond et al. (2008) through an inventory of species living in this environment, and came to the conclusion that treeless open grasslands were formerly restricted in distribution and are mainly recent and anthropogenic. The reason we used their paper as an example of the problem of a continued binary way of thinking around forest and non-forest was because, in their analyses, they divided taxa into two categories following IUCN species assessment. For example:

- 1) In Joseph and Seymour, 2020, Figure 1, there is a comparison of the proportion of endemic Madagascan vertebrate groups, Australian diprotodonts, polyprotodonts, and endemic rodents, as adapted to predominantly forest, grassland, or both habitats. To construct this table, J&S “designat[ed] species as either ‘grassland’ (grassland-limited) or ‘not’ (forest or either habitat)”, i.e., for both countries, the figures for vertebrates add up to 100%, suggesting that vertebrates must be adapted to either forest or grassland or both habitats. It follows then that any species that is adapted to heathland, woodland, savanna, thicket, or any other habitat must have been assigned to the forest or “both” categories. No other habitats were considered or acknowledged, which was why we described the classification as binary.
- 2) Similarly, in Joseph and Seymour, 2021, Figure 2, only two categories are shown, forest-limited or grassland-limited. In the underlying data (Supplementary Table S3C), only these two categories are used and no other habitat types are considered, which is again why we described the classification as binary.

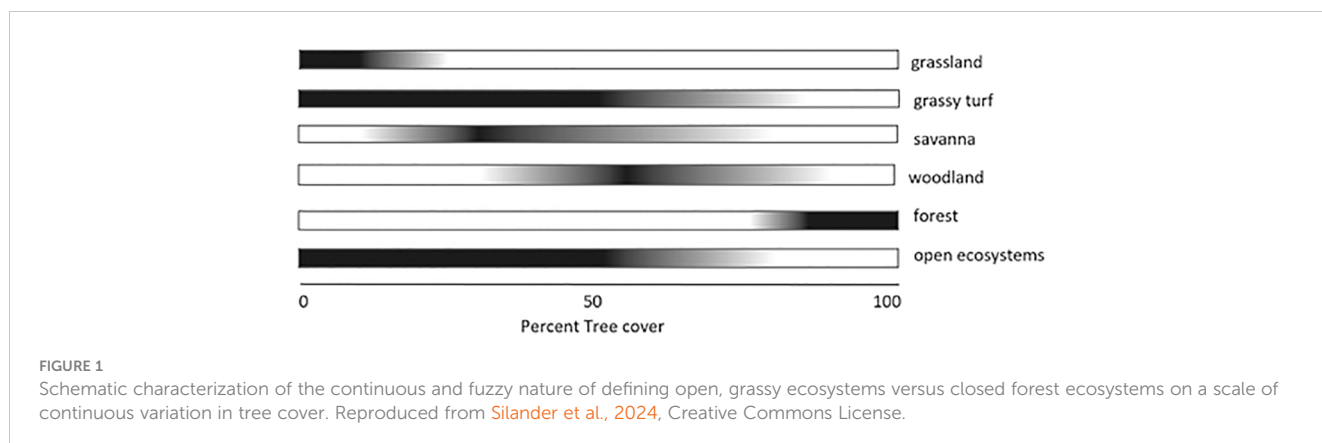
These strict, binary allocations to forest and/or grassland habitats are problematic, because, as acknowledged in Joseph and Seymour, 2024, there are multiple vegetation types present in Malagasy landscapes, most of which comprise a matrix of grassy

and woody elements. True forests are confined to the north east (Straka, 1996; Moat and Smith, 2007), elsewhere found along riverine areas and ravines protected from fire. The dichotomy of open treeless grassland versus true forest when assigning affinities for animals and plants is ecologically inaccurate. A suite of species can exist across the continuum of grassy, open, and mosaic ecosystems, characterized by the presence of C_4 grasses, with degrees of tree cover varying from 0% to 75% (Robinson et al., 2021; Silander et al., 2024). The distinction between true forests and the continuum of other habitats is nicely illustrated in Silander et al. (2024) (Figure 1), reproduced here. This figure demonstrates how the attribution of species to open treeless grasslands versus “forests” is bound to encompass only a very small subset of the suite of species that are adapted to open and mosaic habitats, artificially inflating the number of “forest” species, which in J&S’s analyses (Joseph and Seymour, 2020, 2021) covers the full suite of other habitats that by default must include, heathlands, savannas, open woodlands, and dry forests with a grassy understory. It is in this context that we cited J&S as perpetuating a false dichotomy in our paper (Gillson et al., 2023).

The figures described above (Joseph and Seymour, 2020, 2021) are problematic as they conflate savanna, woodland heathland, and forest, which, as J&S point out in their current commentary (Joseph and Seymour, 2024), have very distinct ecologies. In contrast to the figures, the text of the Joseph and Seymour, 2020, 2021 papers and their current commentary (Joseph and Seymour 2024) acknowledges the presence of landscape mosaics. Habitats other than forest and grassland are shown elsewhere in their work. For example, five vegetation types are mentioned in J&S 2020, Figure 3A and in Figure 3B, and the woodland category is treated separately from forest (as it should be).

In a later paper (Joseph et al., 2022), J&S suggest that the lack of correlation between rainfall and tree cover provides evidence for the effects of anthropogenic fire. However, this decoupling of climate and tree cover is well known in the literature and is explained by the interacting effects of rainfall seasonality, fire, and herbivory which all limit tree cover to varying degrees and cause a non-linear relationship between tree cover and rainfall (e.g., see Bond et al., 2005; Sankaran et al., 2005; Staver et al., 2011; Higgins and Scheiter, 2012). Savannas are likely to occur in areas where rainfall is seasonal (as in the Highlands of Madagascar), as grass biomass accumulates in the wet season, dries out, and burns in the dry season, regardless of human sources of ignition and there being enough annual rainfall to support forest cover. Humans are capable of manipulating this relationship to encourage favoured habitat types (e.g., see Whitlock et al., 2010); however, attempts to suppress fire completely in seasonally rainy savannas have proved largely futile (e.g., see van Wilgen et al., 2004).

The main point in Gillson et al. (2023) is to stress the importance of understanding landscape history and the potential contribution of palaeoecology, especially in countering afforestation schemes that are planned for open and mosaic landscapes erroneously perceived as degraded (Gillson et al., 2023). We do not dispute that deforestation is occurring in some areas of Madagascar (Vieilledent et al., 2018). We also acknowledge the interacting effects of climate and fire from ca. 1,000 years ago that



together increased the proportion of open grassy ecosystems compared with woody habitats. Our intention in advocating the use of palaeoecology is to help find out which areas were formerly forests, which were not, and what the landscape mosaic looked like prior to intensive human impact over the past 1,000 years. None of this runs contrary to the commentary on mosaic landscapes (Joseph and Seymour, 2024) but does highlight our justifiable concern with the figures in the papers we cited (Joseph and Seymour, 2020, 2021). We find some of the generalized statements (e.g., “several lines of evidence affirm the highland grassland is young” (Joseph and Seymour, 2020) that appear in their work problematic. The inference that almost all grasslands and savannas in the Central Highlands are of anthropogenic origin can potentially open the way for afforestation of the Highlands, as anthropogenically derived grasslands are perceived to be of little ecological value (e.g., see Joseph et al., 2022). The risk is that such habitats are assessed as fair targets for introduced fast-growing trees such as *Eucalyptus* and pine plantation instead of species that are native and historically beneficial for communities living around these areas.

Statements attesting to the restricted range and anthropogenic origin of grassy ecosystems do not take into account the range of ancient grasslands (decisively shown in palaeoecological records), grasslands with trees, woodlands, heathlands, and other open habitats (also present in prehuman paleoecological records). We respectfully suggest that if S&J want to avoid misunderstanding of their work, they need to acknowledge the range of vegetation types across the Malagasy highlands. In the case of the figures in Joseph and Seymour, 2020, 2021, we suggest dropping the strict criteria of treeless grassland and including the continuum of habitats mentioned in Silander (Silander et al., 2024). Woodland- and savanna-adapted species need to be removed from the “forest” category. A more representative suite of habitats, as outlined in Silander et al. (2024), that includes true forest as the outlier and the range of open and mosaic habitat types that includes grassland (with or without some trees), savanna, heathland, open woodland will be ecologically more realistic and more in harmony with their current commentary (Joseph and Seymour, 2024).

Meanwhile, our main point stands; palaeoecological data are invaluable to understanding the history of Madagascar’s landscapes but remain relatively scarce (Gillson et al., 2023). In the drier areas, where these debates are most contentious, pollen preservation is often poor and chronologies discontinuous due to hiatuses in sediment deposition. Nevertheless, the records we have provide fascinating insights into the past landscapes of Madagascar (e.g., see Virah-Sawmy et al., 2009a, 2009b, 2016; Razanatsoa et al., 2021, 2022) and the changes taken place prior to human arrival and the interacting effects of climate and humans in shaping the landscapes we see today. Further palaeoecological work and careful interpretation based on knowledge of modern ecological affinities of pollen taxa (see Razafimanantsoa and Razanatsoa, 2024) will help to illuminate questions of how Madagascar’s mosaic landscapes looked and how forested and open landscapes have fluctuated over time in response to changing climate and disturbance by fire and herbivores and since the late Holocene, people. This information will be crucial in halting inappropriate afforestation schemes that utilize non-native species and in ensuring the conservation and restoration of open and mosaic habitats throughout the island.

Finally, the response to our paper and the ensuing academic exchange contribute to the research process, allowing us to refine our arguments and also clarify potential misunderstandings. Such exchanges raise questions regarding how to refine integrated methodologies that address the complexity of Madagascar’s landscapes, and provide a realistic underpinning for the management and restoration of landscapes based on site-specific and historic data. While there appears to be some consensus over complexity of Madagascar’s landscapes, narratives of degradation and economic imperatives continue to shape deforestation and reforestation research questions and methodologies (Gillson et al., 2024). New approaches are needed that are rooted in better exchanges between scientists, historians, and local communities (Gillson et al., 2024). Such exchange will ultimately lead to a better framework of understanding, which will contribute to the management of the island’s biodiversity, improving ecosystem

services in those diverse landscapes that support the needs of its population.

Author contributions

LG: Conceptualization, Writing – original draft, Writing – review & editing. ER: Writing – review & editing. AR: Writing – review & editing. MV-S: Writing – review & editing. AE: Writing – review & editing.

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