

REVIEW

Advancing transdisciplinary research on Madagascar's grassy biomes to support resilience in ecosystems and livelihoods

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Handling Editor: Andrew B. Davies**Abstract**

Grassy biomes (savanna and grasslands) are globally extensive and host a unique biodiversity that is of central importance to human livelihoods. We focus here on the island of Madagascar—a microcosm of the global tropics, covered in 80% grassy biomes—to illustrate how transdisciplinary approaches to research can clarify ecosystem dynamics, from evolutionary history to human land use. Research on Madagascar's human-environment interactions has sparked debates about the role of past and current land use in shaping grassy biomes (e.g., pastoralism, cultivation, fire use). These debates echo those in other regions globally, and highlight obstacles to understanding and supporting both ecosystem and livelihood resilience. Like many tropical biodiversity hotspots, Madagascar faces converging challenges that can be aided by transdisciplinary research, including food and health insecurity, economic inequities, biodiversity loss, climate change, land conversion, and limited resource access. We present a framework to guide transdisciplinary research centered on improved understanding and management of grassy biomes on Madagascar by: (1) establishing a globally common terminology; (2) summarizing data contributions and scientific knowledge gaps relating to Madagascar's grassy biomes; (3) identifying priority research questions for Madagascar with applicability in other regions; and (4) highlighting transdisciplinary, inclusive approaches to research that can co-benefit people and the ecosystems with which they interact.

KEYWORDS

anthropogenic, disturbance dynamics, ecosystems, grassland, grassy biomes, grassy ecosystems, land conversion, land use and land cover change (LULCC), land use, landscape ecology, livelihoods, open ecosystems, savanna

INTRODUCTION

Covering ~40% of the Earth's vegetated land surface (Buisson et al., 2022; Lehmann et al., 2019; Parr et al., 2014), grassy biomes are open landscapes maintained through a combination of climatic forces and disturbance dynamics. Fire, grazing, and human land use regimes modify and maintain grassy ecosystems, which in turn support millions of livelihoods worldwide (Box 1; Bardgett et al., 2021; Lehmann & Parr, 2016; Osborne et al., 2018; White et al., 2000, 1983; Andela et al., 2017). Grassy biomes are fundamental to human well-being globally, and people play diverse roles in shaping these ecosystems, such as managing herbivory through pastoralism, converting land for cultivation, and prescribed burning for a variety of socio-ecological applications (e.g., Alvarado et al., 2018; Berlinck et al., 2021; Buisson, 2019; Di Lernia & Cremaschi, 1996; Marshall et al., 2018; Mistry et al., 2005; Pastro et al., 2011).

Tropical grassy biomes include savannas and grasslands, which became established during the Late Miocene

and Pliocene (8–3 million years ago) through a complex interplay of climate, fire, and herbivory (Bond et al., 2008; Cerling et al., 1997; Edwards et al., 2010; Willis et al., 2008). Despite their relatively young evolutionary age, these ancient grassy biomes can support high levels of biodiversity and endemism (Figure 1; Antonelli et al., 2022; Bond, 2016; Lehmann et al., 2022; Murphy et al., 2016; Parr et al., 2014; Vorontsova et al., 2016), and contribute to shaping biogeographical and biodiversity patterns (e.g., by forming corridors or barriers that can favor differentiation, diversity and micro-endemism between forested areas: Quémère et al., 2012; Sgarlata et al., 2019; Wilmé et al., 2006). Grassy biomes also make major contributions to global biogeochemical cycling (e.g., by holding large amounts of soil and biomass carbon; Abreu et al., 2017; Grace et al., 2006; Jones et al., 2019; Lange et al., 2015; Zhou et al., 2022), and are foundational environments in which much of human evolution and changes in land use (e.g., the development of food production: pastoralism, cultivation) have taken place (Bengtsson et al., 2019; Cerling et al., 2011;

BOX 1

Recommended grassy biome terminology for transdisciplinary communication, building on previously established definitions (e.g., Aubréville, 1957; Aubréville et al., 1958; White, 1983; Moat & Smith 2007), and incorporating consideration of vegetation function (i.e., plant traits reflecting ecophysiological functioning). Terms include recommended ecosystem types (1–3) and disturbance dynamics (8–10). Due to ambiguity between studies, we do not recommend use of “generalized terms” (5–7) unless accompanied by precise open and closed ecosystem terminology; for mixed vegetation types, where applicable, we recommend the term “vegetation mosaic” (4) with ecosystem types specified. Here, we define core terms for grassy biome research, but additional terms (e.g., wetlands) are also relevant as they can support graminoids and herbivore habitats.

1. **Open ecosystem:** (Malagasy*: [vernacular] *hiaka, monto*; French: *milieu ouvert*) Umbrella term for all ecosystems where plants recruit in sunlit environments due to abiotic factors (e.g., climate, soil chemistry, hydrology) that support discontinuous or absent woody cover (trees, shrubs), or edaphic and/or disturbance processes that prevent formation of a closed vegetation canopy. Examples include shrublands, grasslands, and savannas, often maintained by fire and herbivores.

1.1 **Grassy biomes:** (Malagasy*: [vernacular] *fatra, fatrambe, banja*; French: *formations graminéennes; zones herbeuses*) Umbrella term for ecosystems with a continuous grass-dominated ground layer, with or without woody plants (including grasslands and savannas). Grassy biomes often include non-grass species in the ground layer, for example, sedges and a wide diversity of dicots.

1.1.1 **Savannas** (or Savannahs): (Malagasy*: [vernacular] *banja*; French: *savane*) Open ecosystems with a ground layer dominated by herbaceous plants and variable densities of woody plants (trees and shrubs), which are typically maintained by fire and/or herbivory. Herbivores tend to play a greater role in controlling woody cover below climate-potential in drier savannas, while fire typically prevents transitions to closed-canopy ecosystems in wetter regions.

1.1.2 **Grasslands:** (Malagasy*: [vernacular] *bozaka, ahi-dambo***); French: *prairies*) Open ecosystems dominated by a continuous herbaceous layer with little to no tree cover (e.g., prairie, steppe); however, the transition zone between savanna and grassland can be broad. In grasslands, abiotic factors such as cold and frost or seasonally anoxic water-logged soils typically play a major role in limiting tree establishment, with fire and herbivory playing more secondary roles in restricting tree cover. Grasslands frequently have a species-rich and functionally diverse herbaceous plant community, which is often slow to recover after anthropogenic disturbance (e.g., plowing).

2. **Closed ecosystem** (or forest): (Malagasy*: [vernacular] *ala, kirihitra'ala*; French: *milieu fermé, forêt*) Umbrella term for ecosystems with a continuous vegetation canopy dominated by woody species (i.e., forest, thicket, shrubland), which prevents light from penetrating the understory, and a ground layer dominated by fire-sensitive herbaceous cover (which may include C₃ grasses that tolerate low or mixed light) and leaf litter, where seedlings can recruit in the shade. Forest canopies may be seasonally open (deciduous).
3. **Heathlands** (or ericoid thicket): (Malagasy*: [vernacular] *kirihitra, ala-kirihitra, alamaiky, ringy, anjavidy*; Français: *fourré éricoïde*) A shrubland, shrub ecosystem, or closed-canopy dwarf vegetation dominated by ericoids (Ericaceae species) and similar shrubs. Heathlands can occur in various densities and heights, may include occasional trees, and may transition into other ecosystems (e.g., forest, savanna). They are most abundant at higher elevations and latitudes, but can also occur at lower elevations. Heathlands can include a grassy component, but are often too cool, moist, and dense to support C₄ grasses.
4. **Vegetation mosaics:** (Malagasy*: *mifangaro zavamaniry*; French: *mosaïque de végétation*) Generalized term for a mix of two or more functionally distinct ecosystems in a landscape, for example, open and closed ecosystems, or microhabitats characterized by different processes and functions, for example, a mix of forest patches, fire- or grazing-driven grassland, heathland, and patchy transitions along forest or lake margins. Mosaics are often associated with topographic heterogeneity (e.g., variability in local hydrology, geomorphology, slope, soil, microclimate, fire susceptibility, herbivory), but may share some environmental features between vegetation types (e.g., climate, geology, species overlap). The stability and resilience of mosaics vary, especially depending upon the scale of observation.
5. **Woodland:** (Malagasy*: [vernacular] *ala-tapia, ala malalaka; ala ringitra*; Français: *formation arborée*) Generalized term used to refer to ecosystems that contain woody vegetation and are maintained by a

variety of biotic and abiotic factors (e.g., precipitation, seasonality, geology, soils, hydrology, fire, grazing). As functional characteristics central to ecosystem differentiation are often overlooked with this term (Griffith et al., 2017; Ratnam et al., 2011), we recommend avoiding its use without incorporating precise terminology that reflects vegetation function (i.e., vegetation described in terms of “forest” or “savanna” with discussion of relevant disturbance processes). Past applications of this term have varied widely, which can lead to vegetation misclassification, including both open woodlands (savanna) with a fire or herbivory-adapted understory dominated by grasses, and closed woodlands (forest) with a shade-tolerant understory.

6. **Natural vegetation/ecosystems:** (Malagasy*: *zava-maniry voajanahary*, *tontolo voajanahary*; Français: *végétation/ écosystèmes naturel(le)s*) Generalized term for environments that are relatively unmodified by human activity. However, such environments are either extremely rare or nonexistent today, and nuanced land use impacts are often difficult to observe and measure in the past and present (e.g., Phelps & Kaplan, 2017). We instead recommend a pragmatic approach focused on explicit consideration of both land cover and land use: that is, specifying vegetation type (e.g., “forest,” “savanna,” “grassland”) and characterizing the associated processes, heterogeneity, and extent to which humans and other organisms modify or drive biodiversity and ecosystem function (e.g., as in Phelps & Kaplan, 2017). Highly modified environments include, for example, urban areas, monoculture plantations, and anthropogenically denuded landscapes.
7. **Secondary vegetation:** (Malagasy*: [vernacular] *savoka*; Français: *végétation secondaire*) Generalized term for vegetation that replaces a previous form or composition. However, this term is frequently used to describe depauperate or species-poor vegetation that replaces “natural” or a previous form of vegetation through anthropogenic disturbance (e.g., as a result of land clearance for agriculture, charcoal production, or tree plantations). While species-poor vegetation can result from anthropogenic modifications, we do not recommend using “secondary vegetation” to describe species-poor vegetation, as all vegetation has been modified to varying degrees. Instead, we recommend that research focuses on explicitly characterizing land cover (e.g., “forest,” “savanna,” “grassland”) and associated disturbance processes, including the qualities and degree of modification, and how these affect vegetation characteristics (e.g., composition, structure, extent). For example, where forest, savanna, and grassland have been degraded or converted, these areas may be referred to as “degraded,” “converted,” or “species-poor” forest, savanna, or grassland—and described in terms of land use characteristics where relevant (e.g., “rangeland,” “pasture,” “cropland”: Phelps & Kaplan, 2017).
8. **Rangeland** (or pasture): (Malagasy*: [vernacular] *kijana*; French: *pâturage*) Definitions of rangeland and pasture vary widely (Phelps & Kaplan, 2017), but tend to refer to vegetated land used for partial or full grazing/browsing of livestock.
9. **Grazers, browsers, and mixed feeders:** (Malagasy*: [vernacular] *biby mpiraoka ahitra*, *biby mpihinan-javamaniry*; Français: *paisseurs, brouteurs et autres herbivores*) Herbivore diets exist on a continuum from grazing to browsing, with diet preferences determined by physiology and morphology (e.g., dentition and digestion), environmental conditions, and competition. Herbivores that rely primarily on grazing (e.g., sheep, cattle) tend to consume ground cover (graminoid grasses and sedges, herbs), while herbivores that rely primarily on browsing (e.g., folivorous lemurs) tend to consume woody shrubs and trees (e.g., leaves, bark). Mixed feeders (e.g., goats, giant tortoises) consume a combination of these different types of plant foods, and can have highly variable diets.
10. **Fire regimes:** (Malagasy*: *toetry ny afo*; Français: *régimes de feu*) Patterns in fire characteristics (e.g., seasonality, frequency, size, intensity) observable at the landscape scale. For example, landscape-scale fires (>21 ha: Giglio et al., 2018; Phelps et al., 2022) on Madagascar range from large, frequent, and regular at high elevations in the Central Highlands, to relatively small, infrequent, and variable in eastern humid bioclimates (Phelps et al., 2022). Small-scale fires (<21 ha) also have cumulatively important impacts, which vary within fire regimes (e.g., Fernández-García & Kull, 2023; Roteta et al., 2019; Zhao, Li, et al., 2021; Fernández-García, Phelps et al., 2024). Fires can be ignited by people or lightning, with burned area determined by factors such as precipitation, weather, and other forms of disturbance.

*Malagasy terms are drawn from several dialects, reflecting linguistic diversity across the island. We include both scientific terms and a range of vernacular (italics) terms, with further work required to document extensive and variable Malagasy terminologies.

**Note that this term also describes grasses with spiky leaves, such as *Heteropogon contortus*.

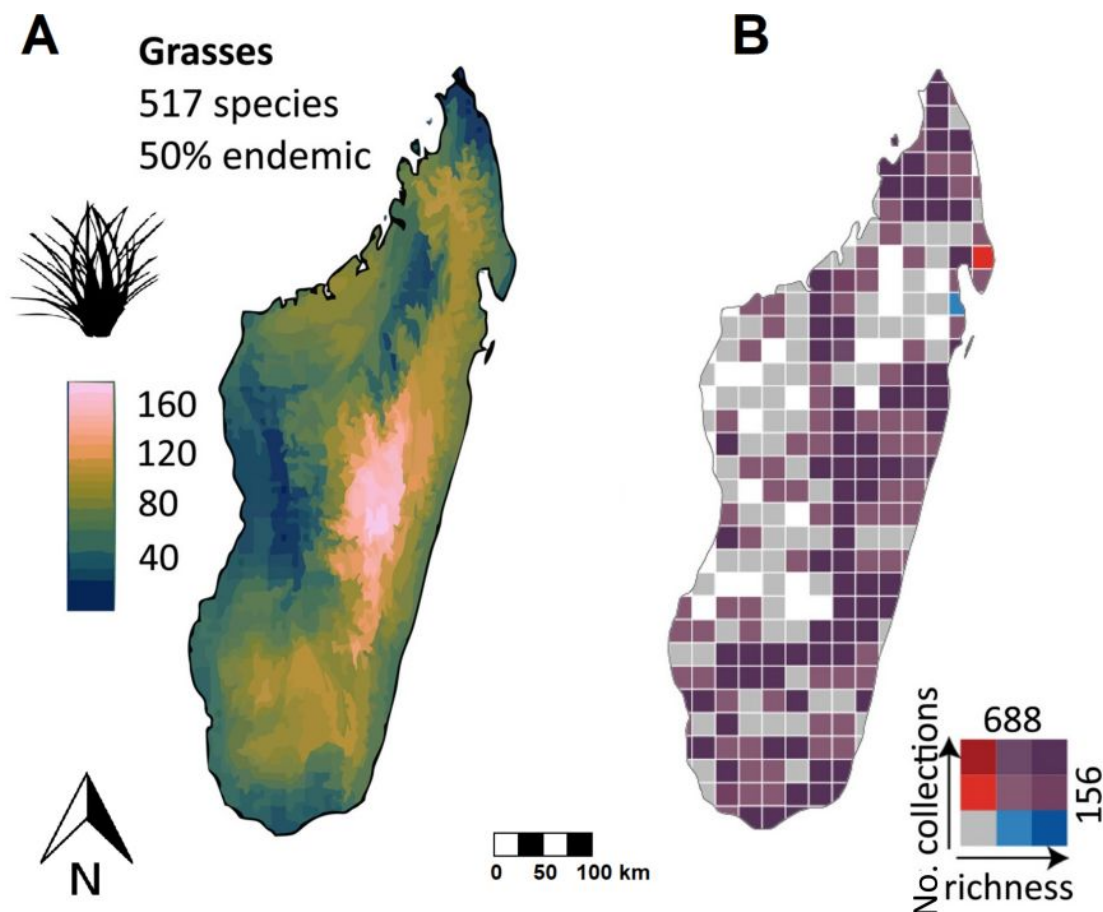


FIGURE 1 Grass (Poaceae) diversity patterns on Madagascar. (A) Species richness based on species distribution modeling with available occurrence records (see Antonelli et al., 2022 for details; 2.5-km² resolution). (B) Numbers of specimen records in herbarium collections and combined number of species, per 50 × 50 km grid cell (white denotes an absence of records). Figure adapted from Antonelli et al. (2022).

Domínguez-Rodrigo, 2014; Potts et al., 2018; Strömberg & Staver, 2022). Yet, grassy biomes are often dismissed as degraded or wasteland, without empirical investigation of biodiversity or land use benefits (Bardgett et al., 2021; Bond, 2016; Parr et al., 2014; Stevens et al., 2022; Strömberg & Staver, 2022).

Livelihood and ecosystem health depend on improved understanding of grassy biome dynamics, as illustrated by Madagascar

Like many biodiversity hotspots, the island of Madagascar is confronted with globally relevant challenges of managing biodiversity conservation and ecosystem function while navigating food and health insecurity, economic inequities, including extreme poverty, rapid population growth, unstable access to resources and international investments, and climate change vulnerability (Barrett

et al., 2011; Carret, 2013; Eckstein et al., 2018; Glamann et al., 2017; Harvey et al., 2014; Herrera et al., 2021; Makoni, 2021; Ralimanana et al., 2022; Scherer et al., 2020; UNICEF, 2021). As of 2021, Malagasy grassy biomes were reported to provision nearly nine million head of cattle (FAOSTAT, 2021), which offer essential support for livelihoods, including household incomes, insurance against crop failure, and are important elements of cultural identity (Steinfeld et al., 2006; World Bank, 2003).

The Holocene expansion of grassy biomes on Madagascar, and Africa more broadly, is often associated with the spread of agricultural land use (i.e., pastoralism and cultivation) and changes in fire and herbivory (e.g., Madagascar: Burney et al., 2003; Burns et al., 2016; Crowley & Samonds, 2013; Godfrey et al., 2019; Razanatsoa et al., 2022; Voarintsoa et al., 2017; Razafimanantsoa et al., 2024; continental Africa: Phelps, Broennimann, et al., 2020; Phelps, Chevalier, et al., 2020). However, the causal interrelationships

between the spread of agriculture and grassy biome expansion are complex and still poorly understood across sub-Saharan Africa, with transdisciplinary research required to disentangle drivers of change, and to advance the understanding of human resilience and adaptation in response to environmental change (e.g., the termination of the African Humid Period, from ca. 5500 years BP: Phelps, Broennimann, et al., 2020; Phelps, Chevalier, et al., 2020; Phelps, Kull, et al., *in press*; Phelps, et al., 2025b). Recent debates about human-environment interactions on Madagascar highlight opportunities and challenges to tropical grassy biome research and management (e.g., debates about the extent of these biomes prior to human arrivals and the role of people and herbivory in shaping the island's grassy biomes: Alva et al., 2022; Dewar et al., 2013; Douglass, Hixon, et al., 2019; Douglass, Morales, et al., 2019; Douglass, Walz, et al., 2019; Godfrey & Crowley, 2016; Gommery et al., 2011; Hansford et al., 2018; Hixon et al., 2018; Joseph & Seymour, 2020; Lehmann et al., 2022; Vorontsova et al., 2016).

On Madagascar and across the globe, pastoralism can occur in virtually any biome (Phelps & Kaplan, 2017), and is associated with pastoral fires, which are often assumed or hypothesized as a primary driver of grassy biome expansion (e.g., Kaufmann & Tsirahamba, 2006; Phelps et al., 2022; Phelps, Broennimann, et al., 2020; Wright, 2017). However, the long-term drivers of vegetation change in grassy ecosystems are complex and debated, especially regarding the role of Holocene human subsistence practices (e.g., pastoralism and cultivation, and associated fire use: Brierley et al., 2018; Crowther et al., 2016; Dewar & Wright, 1993; Godfrey et al., 2019; Hixon, Curtis, Brenner, et al., 2021; Hixon, Douglass, Godfrey, et al., 2021; Hixon, Douglass, et al., 2021; Manning & Timpson, 2014; Phelps, Broennimann, et al., 2020; Wright, 2017). Understanding the long-term drivers of vegetation change is further complicated by recent large-scale land conversion and degradation tied to colonialism, urbanization, population growth, and global market demands (e.g., for Madagascar: charcoal production and logging: Hoang & Kanemoto, 2021; Zhu, 2018; Jarosz, 1993; Kanemoto, 2021; Moser, 2008; Waeber et al., 2015; Vieilledent et al., 2018). Inadequate management of fire risk (e.g., inappropriate fire suppression leading to increased fuel load; lack of infrastructure to contain forest fires) and extreme weather conditions can also cause fire to escape into and damage forest stands, especially when combined with degradation near forest edges (e.g., Cochrane & Bowman, 2021; Kull & Lehmann, 2022; Veldman et al., 2019; Zhao, Yu, et al., 2021).

Combined with the aforementioned factors, limited or patchy palaeo-record coverage across Africa and ambiguities in vegetation definitions also make it difficult to determine the extent of Holocene vegetation change and

the role of human activities (e.g., Fairhead & Leach, 1996; Griffith et al., 2017; Harper et al., 2007; Lambin et al., 2001; Parr et al., 2014; Phelps et al., 2024; Phelps, Broennimann, et al., 2020; Phelps & Kaplan, 2017)—as has been extensively debated for Madagascar—and complicates restoration and conservation targets (Burney et al., 1997, 2003; Bond et al., 2008; Crowley et al., 2021; Godfrey & Crowley, 2016; Vorontsova et al., 2016; albeit see Montade et al., 2024; Razafimanantsoa et al., 2024; Quémère et al., 2012; Salmona et al., 2017; Teixeira, Montade, et al., 2021; Teixeira, Salmona, et al., 2021; Tiley et al., 2022). Furthermore, biogeophysical feedbacks shape grassy biomes in a variety of ways, but their effects are still poorly known (Armitage et al., 2015; Claussen et al., 1999). Many of these are linked to changes in climate, atmospheric CO₂, hydrology, geomorphology, and competition (Armitage et al., 2015; Bond et al., 2003; Bond & Midgley, 2012; Goel et al., 2020; Ramiadantsoa & Solofondranohatra, 2021). Closing these knowledge gaps requires an assessment of research practices on grassy biome dynamics.

We present a framework to advance transdisciplinary research and management of grassy biomes on Madagascar and their relationship to other biomes, including forests. By focusing on Madagascar as a microcosm of the broader tropics (e.g., Phelps et al., 2022; Phelps et al., *in press*), our framework is applicable to other ecosystems across the globe and will shed light on challenges and opportunities faced in grassy biome studies more broadly. In the four sections below, we present our Madagascar-centered framework, which (1) outlines a globally common terminology for grassy biome research, (2) summarizes the contributions, limitations, and knowledge gaps of research on Malagasy grassy biomes with relevance to other regions, (3) identifies priority research questions for Madagascar with applicability in other regions, and (4) highlights transdisciplinary approaches that resolve key knowledge gaps and co-benefit ecosystems and livelihoods. Our framework aims to improve scientific understanding, increase transdisciplinary collaboration, and promote more equitable and sustainable management of grassy biomes on Madagascar and globally.

OUT OF THE WOODS: ESTABLISHING GLOBALLY APPLICABLE, FUNCTIONAL TERMINOLOGY FOR GRASSY BIOME RESEARCH

Transdisciplinary engagement is critical for ecosystem restoration and management (Bowman et al., 2020; Knapp & Collins, 2019; Zhao, Yu, et al., 2021). However, a lack of effective communication across studies,

disciplines, and stakeholders can result in varied terminology and misunderstandings, and detract from scientific advances, inclusive decision-making, and scientifically informed policy advice (Biggs et al., 2022; Davis, 2020a; Descola, 2013; Gardin, 1980; Harris, 2018). For example, assessments of vegetation distribution and the degree to which it has changed over time vary globally due to different definitions and classifications, especially as these relate to disturbance processes such as land use, fire, and herbivory (e.g., Fairhead & Leach, 1996; Griffith et al., 2017; Harper et al., 2007; Lambin et al., 2001; Phelps & Kaplan, 2017). In particular, definitions often focus on vegetation structure or composition (e.g., canopy cover: Dixon et al., 2014) but lack explicit consideration of vegetation function (i.e., plant traits reflecting ecophysiological functioning), which is needed to adequately define ecosystem function and to avoid vegetation misclassification (Keith et al., 2022). Furthermore, the implications of changing vegetation composition and extent can be perceived and valued differently among stakeholders operating at different scales and with different definitions and environmental baselines (e.g., local communities, government officials, conservationists, scientific researchers: Alleway et al., 2023). As a first step toward improving engagement in grassy biome research and management, we summarize (Box 1) and illustrate (Figures 2 and 3) key grassy biome terminology that is globally applicable.

Major debates about the Holocene history of grassy biomes on Madagascar have been fueled by ambiguity

around land cover and land use terms such as “woodland,” “grassy biome,” “savanna,” “grassland,” “(pseudo-)steppe,” “pasture,” “open ecosystems,” “natural,” “ancient,” and “anthropogenic” (Box 1; e.g., Alvarado et al., 2015; Joseph & Seymour, 2020, 2021; Lehmann et al., 2021; Lowry II et al., 1997; Samonds et al., 2019; Solofondranohatra et al., 2020; Vorontsova et al., 2016). These debates reflect pervasive issues with vegetation classifications worldwide, which can stem from difficulties establishing discrete categories for a continuum of vegetation that is: highly variable in space and time; observed with diverse data types and resolutions; and interacting with complex disturbance dynamics that are not easily categorized (e.g., Chazdon et al., 2016; Griffith et al., 2017; Lehmann et al., 2011; Phelps & Kaplan, 2017; Ratnam et al., 2011; Staver et al., 2011). For example, different applications of the umbrella term “woodland” can include or exclude grassy biomes (e.g., “Miombo woodlands” in south-central Africa can occur as savanna or dry forest depending upon disturbance factors). Failure to distinguish between open ecosystems (e.g., heavily wooded savannas, which typically have a shade-intolerant C_4 grassy matrix) and closed ecosystems (i.e., forests, which generally have a sparser understory and do not support C_4 grasses) leads to variability and inaccuracies when calculating deforestation rates and assessing levels of degradation, with major implications for understanding the drivers of vegetation change and developing effective land management strategies (e.g., Bond et al., 2022; Griffith et al., 2017). Furthermore, there is a need for common

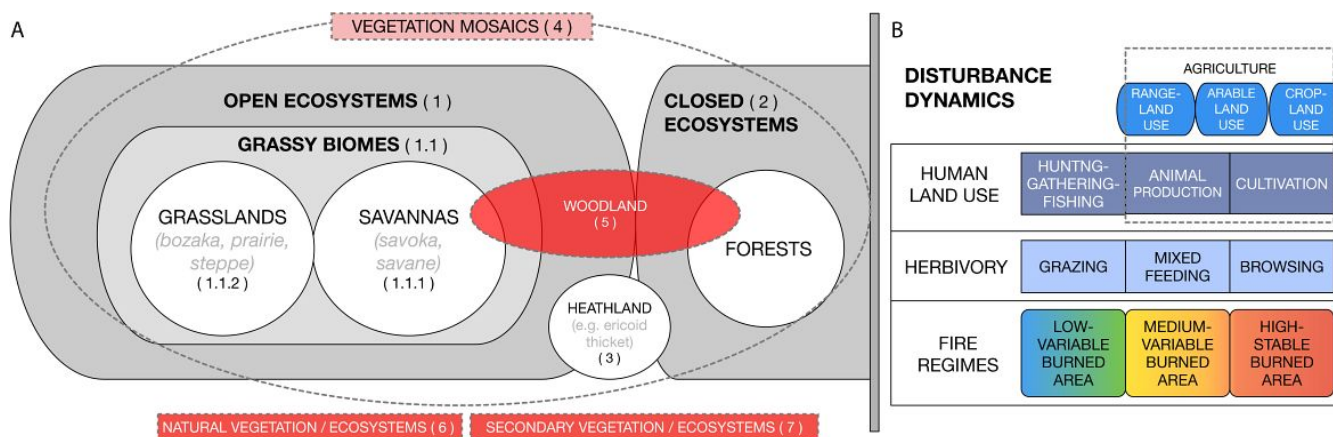


FIGURE 2 Conceptual diagram of key grassy biome terminology (with example illustrations in Figure 3), to navigate pervasive issues with vegetation classifications worldwide (e.g., Chazdon et al., 2016; Griffith et al., 2017; Keith et al., 2022; Lehmann et al., 2011; Phelps & Kaplan, 2017; Ratnam et al., 2011; Staver et al., 2011). Numbers in parentheses correspond to definitions in Box 1. Dotted lines indicate generalized terms, which may apply to closed or open ecosystems. (A) Key vegetation terms and their conceptual relationships. (B) Disturbance dynamics such as human land use, herbivory, and fire, which are conceptually distinct from vegetation cover, and can occur on virtually any vegetation type (Phelps et al., 2022; Phelps & Kaplan, 2017). Ambiguous use of generalized terms such as “woodland,” “natural vegetation,” or “secondary vegetation” (red) can lead to misunderstandings between studies, and are therefore not recommended unless accompanied by precise terminology. Additional ecosystems not mentioned here (e.g., wetlands) are also relevant; a variety of additional factors influence vegetation change in grassy biomes, but are not the focus of this diagram (e.g., climate, soils, geology, atmospheric CO_2).

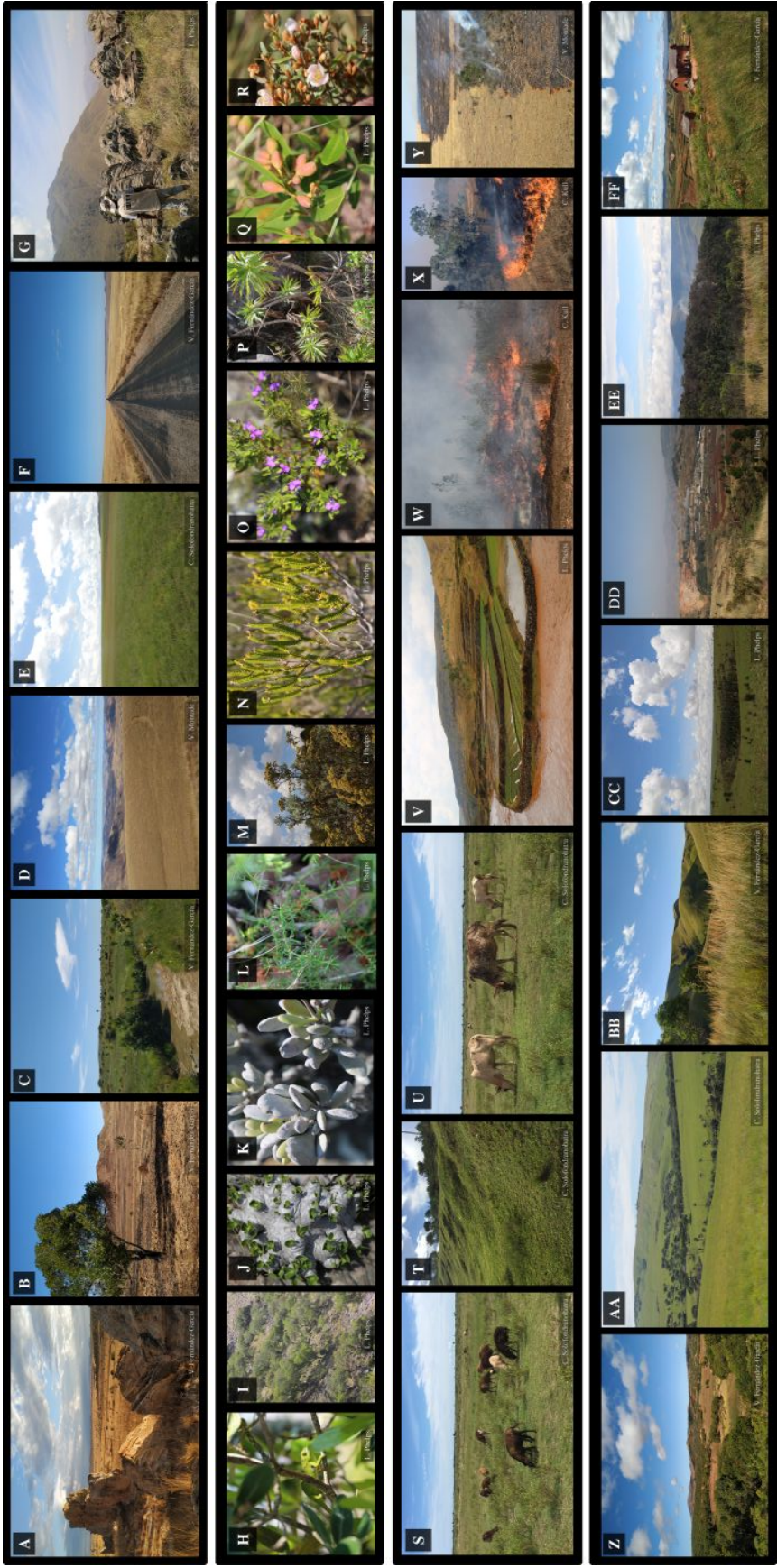


FIGURE 3 (A–G) Examples of grassy biomes in Madagascar’s highlands. (H–R) Diversity of species occurring in Madagascar’s grassy biomes (many endemic), such as (H) chameleons (*Furcifer minor* [tapia, savanna]), (I) fire-adapted savanna trees (*Uapaca bojeri*), (J, K) succulents ([J] *Pachypodium brevicaule*, [K] *Kalanchoe integrifolia*), (L–R) shrubs ([L] *Asparagus madecassus*, [M] *Helichrysum* sp., [N] Ericaceae, [O] *Polygala grandidieri*, [P] *Dialypetalum compactum*, [Q] *Abrahamia ibityensis*, [R] *Xerochlamys bojeriana*), and orchids. (S–Y) Examples of grassy biome disturbance dynamics, for example, (S–U) livestock herbivory, (V) cropland, and (W–Y) fire. (Z–FF) Examples of vegetation mosaics on Madagascar. Photo credits: (A–C, F, Z, BB, FF) Víctor Fernández-García; (D, Y) Vincent Montade; (E, S–U, AA) Cédrique Solofondranohatra; (G–R, V, CC–EE) Leanne N. Phelps; (W, X) Christian Kull.

recognition that vegetation characteristics extend beyond “grasses” versus “trees” (e.g., Crowley et al., 2021; Godfrey & Crowley, 2016; Solofondranohatra et al., 2020; Vorontsova et al., 2016). Grassy biomes can be composed of a wide variety of graminoids (e.g., grasses, sedges), non-graminoid monocots (e.g., lilies, orchids), herbaceous dicots, and woody plants (e.g., geoxyles [underground trees], trees, shrubs). These different types of vegetation support different types of herbivory and have variable tolerance to other kinds of disturbance (Box 1).

Interpretation of the terms “natural,” “ancient,” and “anthropogenic” also vary widely—sometimes treated as overlapping and other times treated as mutually exclusive (Joseph & Seymour, 2021; Marchant, 2021; Marchant et al., 2018; Salmona et al., 2017; Silva et al., 2022; Solofondranohatra et al., 2020). Like all modern biomes worldwide, tropical grassy biomes are human-modified to some degree (Ellis et al., 2021), with a variety of effects on ecosystem function and human livelihoods. Landscapes with apparent anthropogenic modifications are often implicitly assumed to have less biodiversity and lower ecosystem value than landscapes that appear less modified, with local land use practices typically assumed to drive loss of biodiversity and ecosystem function (Cronon, 1996; Ellis et al., 2021; Fletcher et al., 2021; Kull et al., 2013; Taylor & Lennon, 2011). However, empirical investigation of the relationships between disturbance, biodiversity, and ecosystem function is required, as different forms and intensities of anthropogenic disturbance can modify biodiversity and the range of available habitats to varying degrees (e.g., Marshall et al., 2018; Mayor et al., 2012; Siebert & Belsky, 2014; Wurz et al., 2022). This issue thus extends into a political space: if common ground and effective management decisions are to be reached, there is a need for multi-scalar research that offers clear definitions and clarity about the values and assumptions of multiple stakeholders.

CONNECTING SILOS: ESTABLISHING DATA TYPES, CONTRIBUTIONS, AND SCOPE

For Madagascar and the broader tropics, long-standing assumptions that grassy biomes are largely degraded landscapes have prevented investigations of: their origins and antiquity; temporal changes in their composition and extent; their contributions to livelihoods and ecosystem function; and the processes that shape them (e.g., land use, fire, herbivory) (Bond & Parr, 2010). Such assumptions can persist due to:

1. Lack of communication and collaboration among disciplines, which can lead to disconnects between different data sources (e.g., between archaeological and palaeo-records and modern environmental information, which typically cover different spatial and temporal scales: Dietl et al., 2015; Marchant et al., 2018);
2. Limited spatio-temporal coverage of modern grassy biome surveys and palaeo-records (e.g., on Madagascar: Broothaerts et al., 2023; Burney, 1987; Burney et al., 2004; Gasse & Van Campo, 1998, 2001; Hagl et al., 2021; Razafimanantsoa, 2022; Teixeira, Montade, et al., 2021; continental Africa: Phelps, Broennimann, et al., 2020; Phelps, Chevalier, et al., 2020);
3. Limited understanding of how long-term disturbance processes have shaped the composition and extent of grassy biomes (e.g., Lambin et al., 2001; Lehmann et al., 2014; Phelps et al., 2022; Phelps & Kaplan, 2017) and limited transdisciplinary communication about ecosystem dynamics in modern grassy biomes (e.g., Hempson et al., 2015, 2019; Lehmann et al., 2011; Osborne et al., 2018; Phelps et al., 2022);
4. In some regions, limited understanding of grassy biome contributions to human livelihoods and culture, and associated biodiversity: that is, poor ability to distinguish among species-rich and species-poor grassy ecosystems and their livelihood contributions; a tendency to focus on agricultural productivity or biodiversity rather than co-beneficial management of ecosystem function and livelihoods (e.g., Lehmann & Parr, 2016; Martin et al., 2022; Parr et al., 2014);
5. Environmental management practices centered on institutions, training, and discourse that are historically dominated by forestry (e.g., Appendix S1: Figure S1; Bond & Parr, 2010).

To foster transdisciplinary engagement in grassy biome research and management, we focus on the tropical microcosm of Madagascar to summarize the ways in which combining different types of datasets can advance the understanding of spatio-temporal dynamics in grassy biomes (Figure 4; Phelps et al., 2024). These datasets include: archaeological, palaeoecological, botanical, faunal, ethnographic, ethnohistorical, functional trait, genetic, and geomorphological data, along with data obtained from remote sensing and ecological models. It is our hope that this will inspire grassy biome data compilations in other tropical regions as well. Integrating different data types gathered at various spatio-temporal scales, from local to continental and daily to geological (Figure 4), can advance research and management of tropical grassy biomes. Each data type has inherent strengths and limitations (Appendix S1: Table S1), and therefore multi-archive approaches can reduce misinterpretations and advance the

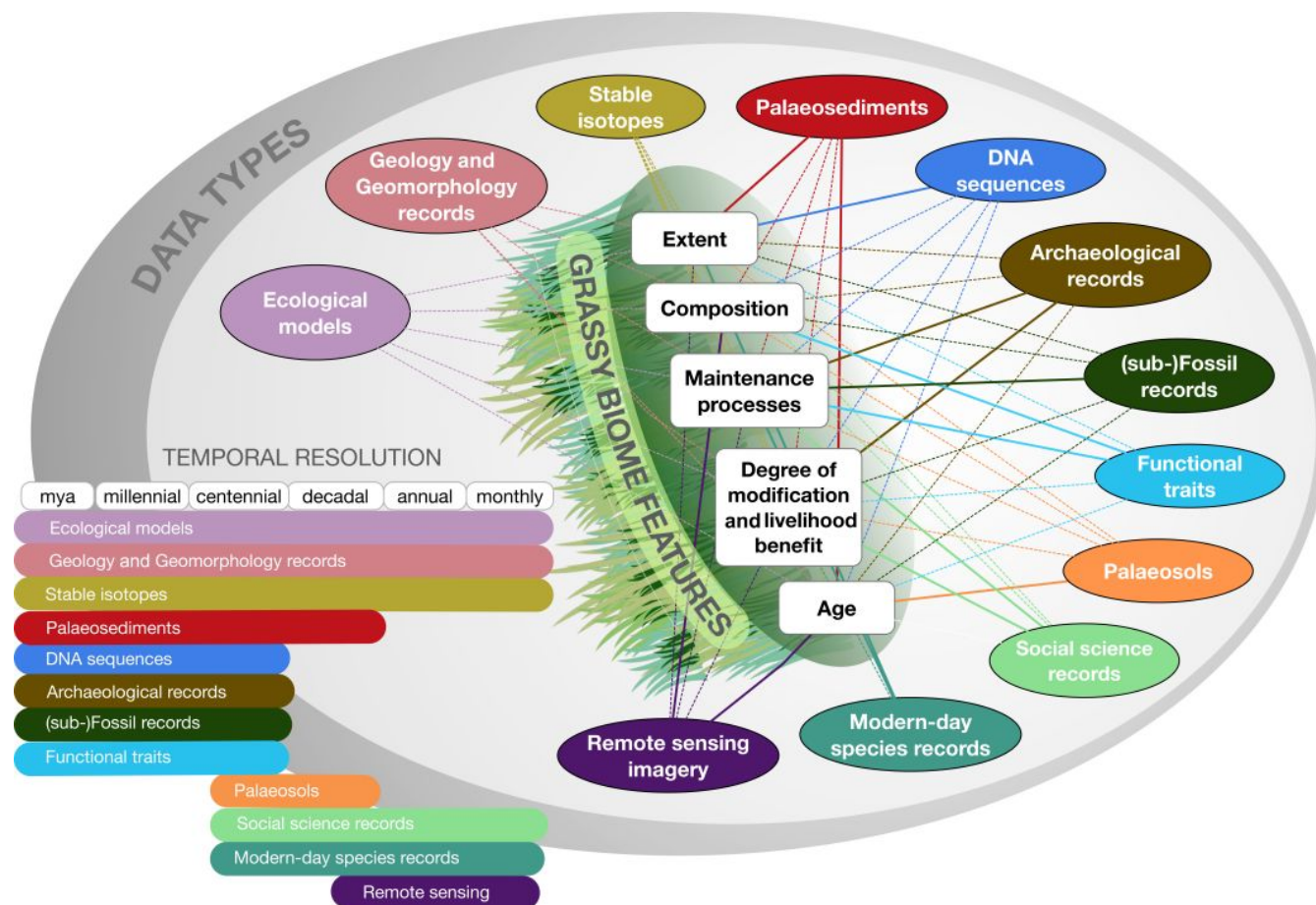


FIGURE 4 Summary of grassy biome data types (Appendix S1: Table S1), their temporal resolution, and relationship to features of vegetation change in grassy biomes. Solid lines: data type provides direct information about a given grassy biome feature; dashed lines: data type offers indirect information about a given grassy biome feature. Some data types can overlap (e.g., for pollen, phytoliths). Illustration credit: Leanne Phelps.

science behind the management of ecosystems and livelihoods.

GREENER PASTURES: TRANSDISCIPLINARY APPROACHES TO GRASSY BIOME RESEARCH, AS ILLUSTRATED BY MADAGASCAR

Effective research and management of grassy biomes requires transdisciplinary approaches that resolve knowledge gaps and foster collaborative and adaptive management of ecosystems and livelihoods. Below, we present 20 key research questions (Figure 5) and three transdisciplinary approaches for advancing our understanding of grassy biomes on Madagascar (Figure 6), which can and should be applied in other regions. Researchers and managers can build on this framework to identify transdisciplinary needs and objectives together with local

stakeholders across the tropics (e.g., community members, conservationists, protected area managers, local governmental officials).

Approach 1: Improve integration of past, present, and future datasets in ecosystems research

Combining a variety of data types can offer context about changes in the extent and composition of biomes through time and the drivers of vegetation change (e.g., Figure 4; Appendix S1: Table S1; Antonelli et al., 2022; Ralimanana et al., 2022). This requires data integration across spatial-temporal scales to clarify how past climates and ecological and anthropogenic interactions shape present and future grassy ecosystems (e.g., Alva et al., 2022; Anderson, 2019; Ardalan et al., 2015; Githumbi et al., 2020; Herrera et al., 2017; Wynne-Jones, 2012). For example, there is some consensus regarding the prehuman presence

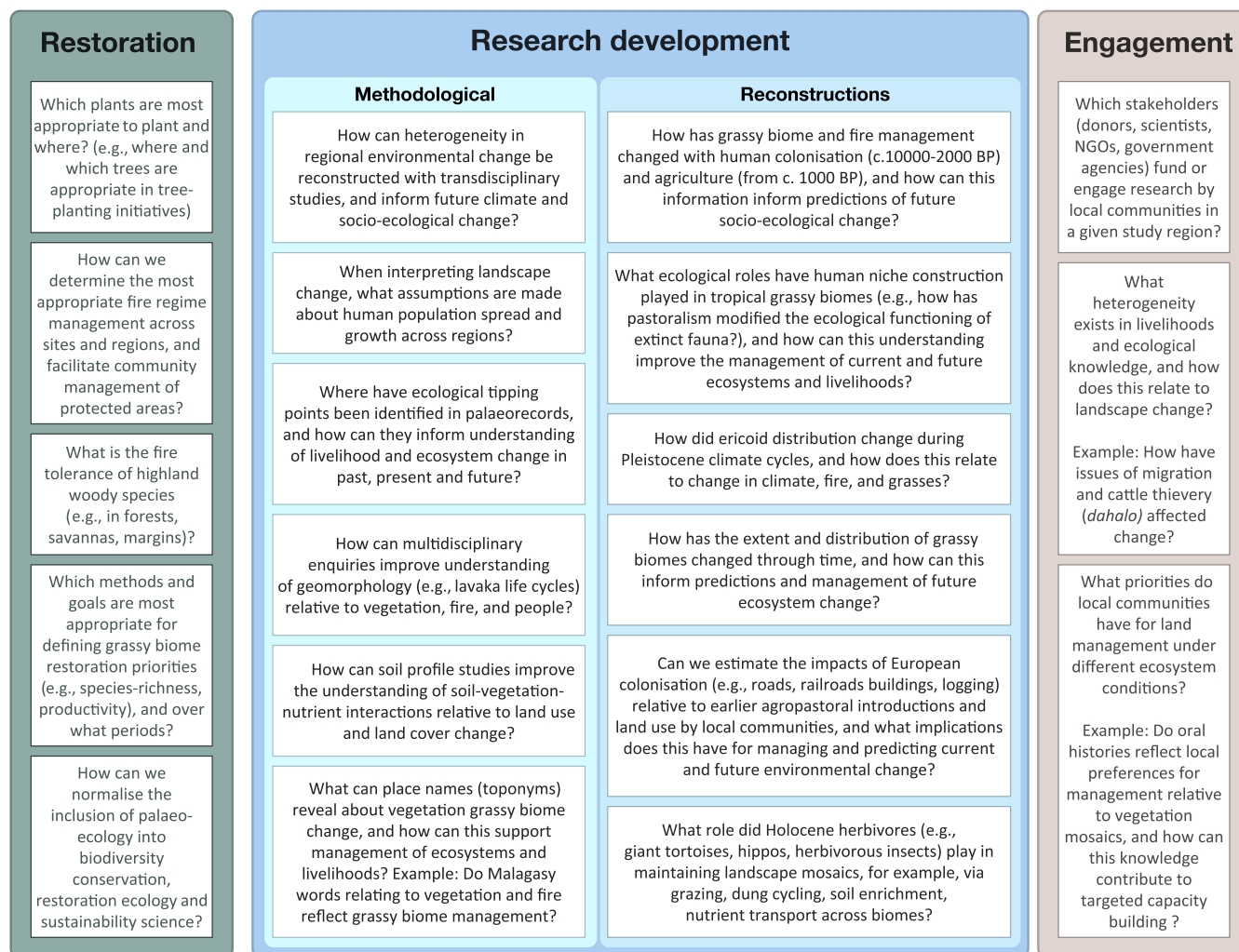


FIGURE 5 Top 20 transdisciplinary research questions focused on Madagascar, and of broader applicability in other regions. Questions were collectively prioritized by the coauthors for future research on Madagascar's grassy biomes (see Appendix S1: Table S2 for further questions). Addressing these transdisciplinary research questions will require integration of past, present, and future information, and their implementation can increase the effectiveness of management practices.

of grassy biomes on Madagascar (Antonelli et al., 2022; Hackel et al., 2018; Lehmann et al., 2022; Vorontsova et al., 2016), but the degree to which human land use has modified their extent and composition is debated—as in sub-Saharan Africa more broadly (e.g., Brierley et al., 2018; Phelps, Broennimann, et al., 2020; Wright, 2017). This knowledge gap is perpetuated by limited spatio-temporal coverage and limited integration of datasets stemming from different disciplines. Improved reconstructions and predictions of grassy biome distribution, composition, and land use are needed to help identify effective conservation priorities and strategies to support ecosystem and livelihood resilience under future ecosystem change. Achieving these will require integration of long-term records with varying spatio-temporal coverage and communication among relevant disciplines (e.g., combining palaeoecological, archaeological, ethnohistorical, evolutionary, and ecological

datasets; Dietl & Flessa, 2011; Willis & Birks, 2006; Phelps, Jousse et al., 2019; Phelps, Chevalier et al., 2019; Phelps, Gravey et al., 2022; Phelps, et al., 2025a).

Expand the spatial and temporal scales of available data

High-resolution, multi-proxy records (e.g., pollen, charcoal, isotopes, phytoliths, non-pollen palynomorphs) with adequate chronological control and comprehensive coverage of recent ecosystem structure, function, and use are needed to disentangle complex spatio-temporal dynamics in grassy biomes. However, the preservation of multi-proxy palaeo-records tends to be favored by particular conditions (e.g., permanently flooded wetland sites, buffered neutral sediments, or sheltered caves), and the

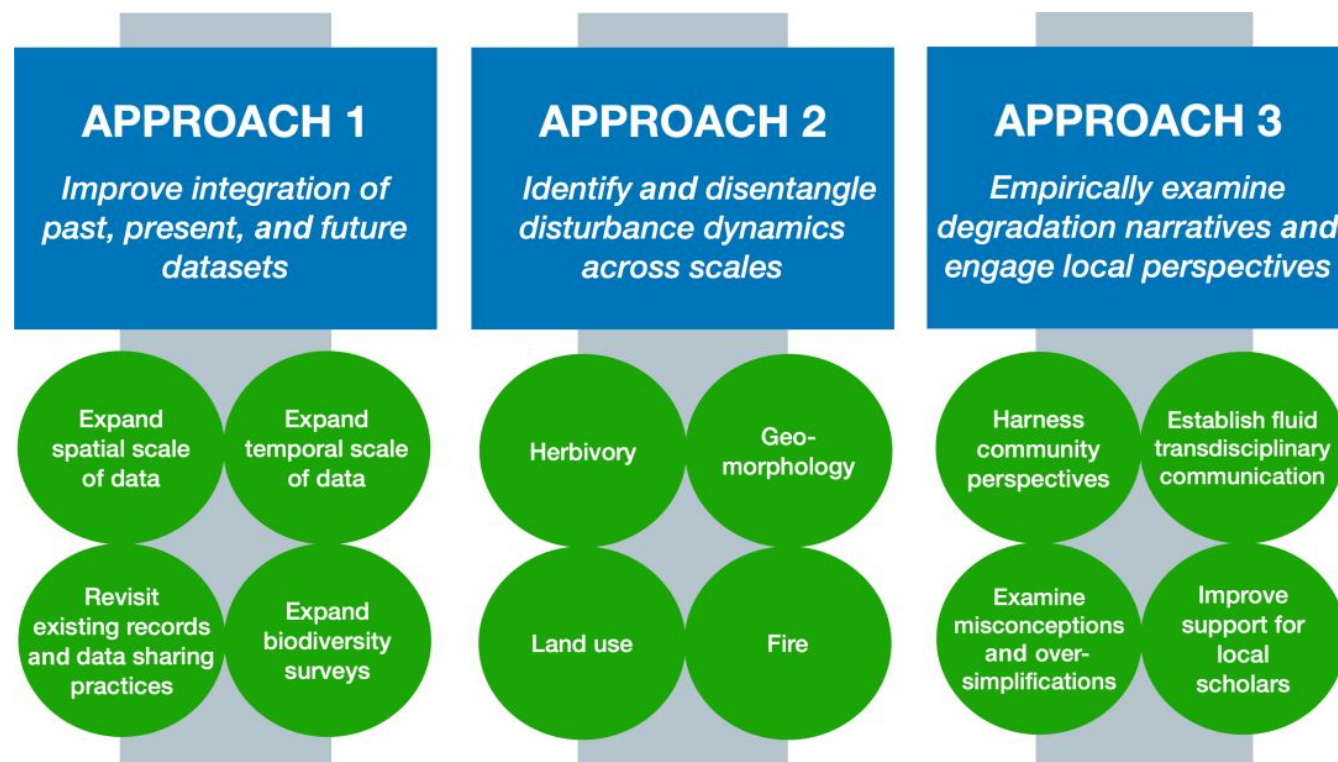


FIGURE 6 Transdisciplinary approaches to advancing research and management of grassy biomes on Madagascar and across the globe.

inaccessibility of some environments limits the spatial coverage of field research. Better incorporation of a variety of survey methods and fossil types that preserve a larger variety of depositional environments can therefore improve the coverage of grassy biome records. These could include expanded sampling of phytoliths, non-pollen palynomorphs, pollen, and macroflora in palaeosols and palaeo-sediments (Strömberg, 2011), and the application of expert knowledge around non-grass pollen indicators (e.g., Phelps, Chevalier, et al., 2020). Aside from select long-term sedimentary and speleothem records (e.g., Broothaerts et al., 2023; Razafimanantsoa et al., 2024; Burney, 1987; Burns et al., 2022; Gasse & Van Campo, 2001; Scroxton et al., 2019; Teixeira, Montade, et al., 2021), most palaeoenvironmental and palaeoclimate records on Madagascar are also limited to the Late Holocene (from ca. 4200 BP; Walker et al., 2019). There is a need for better spatial coverage of longer term records and higher resolution multi-proxy data documenting climate and environmental variability at different scales and under a variety of conditions. One route to better integrating past, present, and future information is to focus research efforts on sites where transdisciplinary, high-resolution datasets can be generated through collaborative, long-term research projects (e.g., Montade et al., 2024; Teixeira, Montade, et al., 2021). By focusing efforts

toward improved communication among researchers working at similar locations, we can develop high-resolution analyses to maximize the understanding and management of grassy biomes at different spatio-temporal scales. In addition, it is critical that well-constrained age models are developed that enable inter-archive and inter-site comparisons (e.g. Godfrey et al., 2019); such knowledge is critical for disentangling the drivers of past environmental change and developing accurate estimates of ecosystem change.

Knowledge of the distribution of archaeological settlements and land use change on Madagascar is also limited, with nearly three quarters of the island under-investigated (e.g., in terms of limited survey and excavation, available data, and active field archaeologists; Davis, DiNapoli, et al., 2020; Davis, Andriankaja, et al., 2020). More investigation of historical settlement and land use is required to estimate the effects of past human activities on vegetation change, including food-producing, food-gathering, and associated fire practices. Increasing the spatio-temporal scale and integration of contemporary, historic, and palaeo-records will improve the understanding of livelihood resilience and lead to better predictions of future ecosystem change across heterogeneous landscapes. With improved, cumulative records of land use change, we can also assess the degree to which anthropogenic

landscapes are stable ecological components or constitute unstable and emerging ecosystems. For example, to clarify past demographic changes and spatio-temporal dynamics of human and agricultural arrivals on Madagascar, we need to expand archaeological investigations and combine them with additional data, such as demographic inferences based on genetic and genomic data (e.g., Alva et al., 2022; Ardalan et al., 2015; Douglass, Hixon, et al., 2019; Douglass, Morales, et al., 2019; Douglass, Walz, et al., 2019; Hansford et al., 2018; Herrera et al., 2017; Kusuma et al., 2015). Combining archaeological and genetic information with Holocene sedimentary records from lakes, marshes, and wetlands is also crucial for disentangling the drivers of vegetation change, as this provides a deep-time perspective capable of identifying temporal lags in human-environment-climate effects (e.g., Chikhi & Sgarlata, 2022; Li et al., 2020; Quémère et al., 2012; Razanamahandry et al., 2022; Razanatsoa et al., 2022; Salmona et al., 2017; Teixeira, Montade, et al., 2021; Tiley et al., 2022; Virah-Sawmy et al., 2010; Voarintsoa et al., 2017).

Revisit existing records and improve data sharing practices

Reanalysis, reevaluation, and synthesis of existing and new datasets can improve our ability to reconstruct and predict ecosystem change (Davis, 2020a, 2020b; Davis, Andriankaja, et al., 2020; Davis, DiNapoli, et al., 2020; Douglass, Hixon, et al., 2019; Douglass, Morales, et al., 2019; Douglass, Walz, et al., 2019; Gaillard et al., 2008; Hixon et al., 2022; Phelps, Broennimann, et al., 2020; Phelps, Chevalier, et al., 2020; Ullah, 2015). For instance, synthesis and calibration of palaeosedimentary and archaeological chronologies within and across study sites can clarify the timing and drivers of landscape and vegetation change (e.g., Burney et al., 2003; Godfrey et al., 2019; Phelps, Chevalier, et al., 2020; Stephenson et al., 2021), and improve reconstructions of human demographic change (Douglass, Hixon, et al., 2019; Douglass, Morales, et al., 2019; Douglass, Walz, et al., 2019; Manning & Timpson, 2014). When combined with insights from current socio-ecological contexts and historical sources (e.g., remote sensing, social surveys, genetic and functional trait data, ethnohistorical records), these syntheses can offer deeper understanding and novel interpretations of existing records and past variability, as well as improve predictions of current and future ecosystem change (e.g., Breeze et al., 2015; Coelho et al., 2021; Davis & Douglass, 2020; Quémère et al., 2012; Solofondranohatra et al., 2020). Models based on diverse datasets (e.g., species distribution models, land use change models, dynamic vegetation models, population genetics models), and new statistical

(e.g., simulation-based inference, machine learning) and collaborative approaches (e.g., participatory modeling, open source code and data sharing) can also offer novel insights into ecosystem change (Andermann et al., 2022; Brierley et al., 2018; Chikhi & Sgarlata, 2022; Manning & Timpson, 2014; Phelps, Broennimann, et al., 2020; Phelps, Chevalier, et al., 2020; Salmona et al., 2017; Schüssler et al., 2020; Teixeira, Montade, et al., 2021). These approaches to integrating data from various sources and spatio-temporal scales can allow us to: (1) understand the potential lag effects between human activities and their modifications to grassy biome composition and extent; (2) evaluate the degree to which spatio-temporal biases in existing datasets may influence interpretations of vegetation change; (3) extrapolate multi-scalar patterns from local-scale information (e.g., ecosystem expansions and contractions through deep time); and (4) simulate potential future grassy biome conditions.

Open and efficient data sharing practices among research disciplines and teams is key to the integration of past, present, and future information and can permit environmental characterization and comparison among regions, time periods, and disciplines. Oppositely, poor data sharing practices can limit reconstructions and predictions of ecosystem change, in both scale and accuracy. A number of global repositories now exist, through which individual researchers can openly access and share their datasets and support regional compilations of published data (e.g., Neotoma, APD, NOAA Palaeoclimatology Database, PANGAEA, SISAL, Dryad, IsoMad, ENA: Hixon et al., 2024; Hooghiemstra et al., 2006; Phelps, Broennimann, et al., 2020; Phelps, Chevalier, et al., 2020; Vincens et al., 2007). However, global inequities in access to scientific publishing and infrastructure can lead to regional disparities in the production and access to scientific knowledge (e.g., Vorontsova et al., 2020) and require targeted efforts to improve access and regional representation (e.g., Open Research Africa; African BioGenome Project).

Expand biodiversity surveys

Relationships between grasses and extinct megafauna on Madagascar (e.g., elephant birds, tortoises, and pygmy hippopotamuses) have received extensive research attention and debate in recent years (e.g., Bond et al., 2008; Crowley et al., 2021; Crowley, Godfrey, et al., 2023; Hixon et al., 2024; Godfrey & Crowley, 2016; Hagl et al., 2021; Hansford & Turvey, 2022; Joseph & Seymour, 2021; Nanjarisoa et al., 2017; Rakotomalala et al., 2022; Solofondranohatra et al., 2020; Tiley et al., 2024). However, relationships between invertebrate and plant biodiversity (e.g., butterflies, termites, ants, earthworms, grasshoppers) are under-explored

(e.g., Bond et al., 2022; Iannella et al., 2019; Vorontsova et al., 2020). Expanded field surveys are needed to better establish habitat associations for multiple taxa and groups in different grassy biomes. Lack of plant taxonomic expertise is also a hindrance to evidence-based management and conservation strategies across the globe (e.g., Ahrends et al., 2011). Few Malagasy botanists specialize in grass identification, with the number of grass specialists increasing from zero in 2010 to eight in 2022 (M.S. Vorontsova, personal communication). Even fewer botanists specialize in other grassy biome plants (e.g., herbaceous dicots, ericoids, sedges, non-graminoid monocots such as lilies and orchids, and geoxyles). Moreover, the taxonomy of heaths (Ericaceae) on Madagascar is out of date, with ongoing research aiming to address this knowledge gap (e.g. Hackel et al., 2024). In particular, the genus *Erica* is likely key to understanding grassland-shrubland-savanna dynamics, but the genus is poorly represented in herbaria. Investment in training and resources, for example, for specimen collections and to support Malagasy taxonomists, should be a priority.

Research on the distribution, abundance, and demography of plants and animals associated with forests or open ecosystems in the past and present can also illuminate landscape history, especially where they present as mosaic landscapes; however, studies on these topics have been geographically biased toward northern Madagascar (but see Andriambelason et al., 2021; Godfrey et al., 2021), and taxonomically biased toward rodents, lemurs, and trees (e.g., Andriambelason et al., 2021; Chikhi & Sgarlata, 2022; Crowley et al., 2018; Muldoon et al., 2017; Quémère et al., 2010, 2012; Rakotoarisoa et al., 2013; Salmona et al., 2017, 2020, 2023; Teixeira, Montade, et al., 2021; Teixeira, Salmona, et al., 2021; Tiley et al., 2022). Future research needs to cover more regions and taxa. There is also a need for natural history research to develop realistic parameter estimates for demographic studies (e.g., generation time and mutation rate: Tiley et al., 2020), and for studies of related plant and animal genomes that can help to calibrate the timing of demographic changes for human-introduced species (e.g., bushpigs, rats, cats, dogs, banana, taro, rice, yam, coconut, sorghum, sugar cane, indian saffron, and possibly guinea fowl: Ardalan et al., 2015; Balboa et al., 2024; Beaujard, 2011; Blench, 2010; Crowther et al., 2016; Goodman et al., 2013; Herrera et al., 2017; Hixon, Curtis, Brenner, et al., 2021; Hixon, Douglass, Godfrey, et al., 2021; Hixon, Douglass, Hixon, et al., 2021; Kull et al., 2012; Kusuma et al., 2015; Lee et al., 2020; Sauter et al., 2020). Such data may be instrumental in reconstructing the spatio-temporal extent, diversity, and demographic history of extinct species that may have used or maintained open habitats prior to human colonization of Madagascar (e.g., hippopotamuses, elephant birds,

tortoises; Hansford & Turvey, 2022; Kehlmaier et al., 2023). Increased availability of reference “barcode” DNA sequences and environmental DNA from soil or feces can also improve the identification of species overlooked in biodiversity surveys (e.g., distinguishing grass species; Ragupathy et al., 2009). With the use of ancient DNA, these approaches can extend back in time to reveal past vegetation and faunal dynamics (Orlando et al., 2021; Pedersen et al., 2015).

Approach 2: Identify and disentangle disturbance dynamics and biogeophysical feedbacks across spatio-temporal scales

Globally, disturbance dynamics (e.g., land use, herbivory, fire) and a variety of other factors (e.g., atmospheric CO₂, geomorphology, hydrology) have substantial and variable impacts on grassy biome form and function (e.g., Archibald et al., 2019; Armitage et al., 2015; Bond et al., 2003; Bond & Midgley, 2012; Claussen et al., 1999; Goel et al., 2020; Lehmann et al., 2011; Ramiadantsoa & Solofondranohatra, 2021), but these are difficult to disentangle and are poorly accounted for in estimates of vegetation change. Effective ecosystem management is therefore limited by poor understanding of how different disturbance dynamics interact with flora, fauna, geomorphology, and soils over millennial scales and how these dynamics influence the extent and composition of grassy biomes. In particular, there is a need to better understand how different land use systems have interacted with fire and vegetation change in the past and present (e.g., Archibald et al., 2019; Phelps & Kaplan, 2017).

Disentangling the drivers of change in grassy biomes requires analysis of multiple study sites with a broad range of independently derived palaeoenvironmental proxies (e.g., pollen, charcoal, XRF spectra, isotope and other biomarkers, grain size, diatoms: Broothaerts et al., 2023; Mayle & Iriarte, 2014). To address disconnects in the spatio-temporal scales of palaeo- and present-day ecological information, functional ecology experiments and high-resolution palaeo-records are critical for interpreting long-term disturbance dynamics in grassy biomes. Research on long-term disturbance dynamics in key grassy biome regions, such as Madagascar’s Central Highlands, can facilitate adaptive and effective grassy biome management with co-benefits for biodiversity, ecosystem function, and human livelihoods. Geochemical analyses of sediment and soil samples (e.g., elemental and isotopic composition, radiocarbon dating) can also help with reconstructing recent and long-term links between vegetation, climate, fire, and land use across diverse landscapes (e.g., Razafimanantsoa, 2022; Razanamahandry et al., 2022).

Herbivory

Existing research on Madagascar's grassy biomes demonstrates a critical need to better understand how herbivores may have influenced vegetation composition and extent prior to human colonization, and how this relates to human arrivals, subsequent environmental changes, and modern ecosystem functioning (Burney et al., 2003; Godfrey et al., 2019; i.e., domestic animals from c. 1200 BP and cultivation from c. 1000 BP; e.g., Crowther et al., 2016; Dewar & Wright, 1993; Razanatsoa et al., 2022). Understanding of changing faunal diets, habitats, and ecology can be facilitated through expanded research around isotopes (e.g. Phelps, et al., 2025b), faunal morphology and feeding behavior, coprophilous fungi, plant functional traits, genetic and genomic data, and a variety of modeling approaches. Grassy biome management on the island can also be improved by investigating the roles of wild and domestic fauna in driving Holocene vegetation dynamics, and comparing these with African savanna ecology more broadly (Pringle et al., 2023), particularly regarding changes between herbaceous (e.g., grasses, sedges, and herbaceous dicots) and woody vegetation (e.g., trees, shrubs).

Many isotopic studies on Madagascar have focused on the relative proportions of C_3 versus C_4 plants in extinct megafaunal diets (e.g., Crowley et al., 2021; Godfrey & Crowley, 2016; Hixon, Curtis, Brenner, et al., 2021; Hixon, Douglass, Godfrey, et al., 2021; Hixon, Douglass, et al., 2021). This work is based on the premise that trees, shrubs, and herbs use C_3 photosynthesis while most tropical grasses use the C_4 photosynthetic pathway. However, open biomes can include both C_4 and C_3 taxa, requiring expanded spatio-temporal investigation of a variety of grassy biome plants (e.g., Bond et al., 2008; Hempson et al., 2015). Further, most work characterizing the isotopic signatures of modern vegetation has focused on vegetation outside of Madagascar's grassy biomes (but see Crowley, Schmidt, et al., 2023). More research is therefore needed to characterize the isotopic signatures of plants in Madagascar's open environments (especially for a range of grasses, herbs, sedges, and ericoids); these data can, in turn, be used to reconstruct presence, and possibly relative abundance, of different types of vegetation in the past using pollen, phytoliths, speleothems, soil organic matter, osseous tissues from herbivores, and other proxies (e.g., Aleman et al., 2012; Crowley et al., 2021; Faina et al., 2021; Hixon, Curtis, Brenner, et al., 2021; Hixon, Douglass, Godfrey, et al., 2021; Hixon, Douglass, et al., 2021; Razanamahandry et al., 2022). Expanding this research will also enable comparison of grassy ecosystems between Madagascar and other parts of the tropics (e.g., Bakker et al., 2016; Gill, 2014; Staver et al., 2021; Phelps, et al., 2025b).

Improved understanding of herbivore dynamics can also come from “cafeteria” experiments, which investigate the dietary preferences of herbivores when presented with different environments and food choices (e.g., Burleigh & Arnold, 1986; Cerling et al., 2008; van der Sluis et al., 2014), with the caveat that extant fauna and environments may not be exact analogues for extinct megafauna and the conditions they experienced. Aldabra tortoises were recently introduced in northwest Madagascar (Anjavy reserve) and may provide an ideal case study for such experiments (Pedrono et al., 2020). Documentation of the spectrum of functional traits that reflect herbivore attraction to, and avoidance of, different types of plants within grassy biomes (e.g., grasses, herbs, sedges, trees, and shrubs, including succulents and ericoids) would be particularly informative (e.g., Archibald et al., 2019). Further research on fire-herbivory interactions and how these relate to biodiversity is also needed to understand and maximize benefits among livelihoods, ecosystem function, and biodiversity (e.g., Hempson et al., 2019; Martin et al., 2022).

Fire

There is an increasing need to determine and calibrate recent and past fire regimes on Madagascar (e.g., relating to fire emissions and carbon storage: Hawthorne et al., 2018), clarify the processes that have shaped them through time (e.g., changes in climate, vegetation, land use, and herbivory), and evaluate how they relate to tropical fire regimes more broadly (e.g., Case & Staver, 2016; Laris et al., 2020; Phelps et al., 2022; Singh et al., 2023, 2024). In particular, studies on the relationships between fire regimes, small-scale fires, and the complex drivers of landscape degradation are needed. For recent decades, remote sensing information (e.g., MODIS-derived burned area products: Giglio et al., 2018) has facilitated characterization and comparison of fire regimes at the landscape scale (e.g., Phelps et al., 2022). The increasing availability of high-resolution satellite images (e.g., Sentinel-2 since 2015) has also enabled detection of small-scale fires, which can cumulatively make up large portions of burned area (Fernández-García & Kull, 2023; Ramo et al., 2021; Roteta et al., 2019; Fernández-García, Phelps et al., 2024).

Knowledge of ancient fire regimes is considerably more limited. New studies and methodological applications are required to link long-term fire patterns to adaptive fire management strategies today (e.g. Novenko, et al., 2022a; Novenko, et al., 2022b). For example, high-resolution charcoal analysis of palaeo-sediments and soils can help to disentangle Holocene changes in fire-human-vegetation

relationships (e.g., fire intensity; Hawthorne et al., 2018; Mustaphi et al., 2022). These long-term data will help improve predictions of future fire-vegetation relationships, which are central to informing decisions around fire risk associated with land conversion, tree planting, and ecosystem restoration (e.g., balancing essential timber and fuel wood while ensuring careful management of high flammable species; Kull, 2004; Phelps et al., 2022; Veldman et al., 2019).

Land use

Combined with empirical investigation of fire, herbivory, and biodiversity patterns, improved characterization of land use processes in the past and present can help to maximize benefits between livelihoods and ecosystem function (Phelps & Kaplan, 2017; Phelps, Chevalier et al., 2020; Phelps, Broennimann et al., 2020; Phelps, Davis et al., *in press*; Morrison et al., 2021), e.g., by accurately predicting ecosystem change, informing ecosystem restoration efforts through participatory land use mapping, and developing adaptive land management strategies. In particular, despite being central to human livelihoods, animal husbandry is often overlooked in studies of land use and land cover change, due to lacking characterization of land use systems and poor differentiation between land cover and land use (Phelps & Kaplan, 2017). Improved coverage of social science surveys and ethnohistorical records can help to clarify the functions, cultural significance, and distribution of different land use practices, as well as how land use interacts with biodiversity and ecosystem function across heterogeneous landscapes (e.g., ethnographic, ethnobotanical, and economic-demographic-livelihood; e.g. Randall, 2015).

Geomorphology

Evaluating changes in landforms over different time scales can provide insight into past changes in vegetation cover and land use (e.g. Liu et al., 2024). Erosional gullies, called lavaka (meaning “hole” in Malagasy), are the most visible aspect of hillslope erosion on Madagascar. They were prominent before human arrivals, and may be particularly informative (Mietton et al., 2006, 2014; Wells & Andriamihaja, 1997). In other regions, erosional gullies can also be referred to as Vocolocas (i.e., in Brazil: Chaves, 1994; Vieira, 2008), or beng gang (i.e., in China: Jiongxin, 1996; Liao et al., 2019; Wei et al., 2021). Although initial work has established the broad-scale controls of lavaka formation and dynamics on Madagascar (e.g., Broothaerts

et al., 2023; Brosens et al., 2022; Brosens et al., 2023; Cox et al., 2010; Cox, King Phillips et al., 2024; Wang et al., 2021; Wells & Andriamihaja, 1997), few studies have quantitatively and critically addressed questions about their long-term development, including the role of different human land uses, and how lavaka formation processes relate to other aspects of erosion and landform change (e.g., Gosling et al., 2012; Scholtz et al., 2014; Zhou et al., 2022). For example, Brosens et al. (2022) estimated that the number of erosional gullies in the Lake Alaotra region (northeast Central Highlands) grew rapidly from 1949 to 2010 CE and inferred that the regional rate of lavaka formation and sediment loss increased around the same time as human settlement, ca. 1000 BP. However, longitudinal analysis contradicts these findings, showing instead that lavaka erosional activity decreased in the same area and over the same time period (Cox, King Phillips, et al., 2024).

There are many uncertainties in the understanding of lavaka life cycles, and of gullies in general; these can vary (sub-)regionally (Voarintsoa et al., 2012), and are not sufficiently constrained to ensure reliable model outputs. Studies on the long-term rates of lavaka formation and stabilization are needed that can contextualize recent rates of vegetation change and soil erosion using aerial photography, satellite imagery, isotopic analysis (e.g., Igbokwe et al., 2008; Mabit et al., 2018). Future approaches could include mass-balance modeling to test landscape stability, which requires reliable data on volume losses and landscape lowering rates (e.g., Brosens et al., 2023).

Equally important is the analysis of how lavaka dynamics impact land use, soil, and vegetation change; and analyzing human interactions with lavaka is required to understand spatio-temporal heterogeneity in their historical relationships (e.g., Razanamahandry et al., 2022). Recent work has found that lavaka provide patch environments and fire refugia for trees and shrubs in the grassy highlands (Cox, Carrère, et al., 2024). However, the extent to which Malagasy farmers integrate lavaka into their land husbandry, taking advantage of higher moisture levels and more fertile substrates, is only now beginning to be examined (Cox, Carrère, et al., 2024). Knowledge is also still limited regarding how geomorphological change on Madagascar shaped biodiversity patterns in grassy biomes before human arrival (Stephenson et al., 2021). It is clear, however, that narratives of human causation for geomorphologic change—on Madagascar and in other former European colonies—are often oversimplified, as the geomorphology, geology, soils, vegetation, and land use are highly complex and multi-factored, requiring improved documentation (e.g., Collins et al., 2022; Cox, Carrère,

et al., 2024; Cox, King Phillips, et al., 2024; Crowley & Sparks, 2018; Dewitte et al., 2013; Lehmann et al., 2022; Vågen, 2006; Voarintsoa et al., 2012). Useful future studies will investigate how a variety of geomorphic factors have affected Holocene vegetation dynamics and clarify the roles that people have played.

Approach 3: Empirically examine degradation narratives and engage local perspectives in scientific research

There is a need to shift scientific narratives and communication away from widespread simplistic assumptions, and toward empirical and nuanced investigation of the complex drivers underpinning vegetation change and landscape degradation (e.g., fire-degradation relationships across ecosystems: Bliege Bird et al., 2020; Kull, 2000; Phelps et al., 2022). This will not only deepen the understanding of vegetation change and guide land management, but also encourage scientifically informed exchanges between researchers, policy makers, and those living in and interacting with grassy biomes. There is a perpetual need for collaboration between researchers and local, regional, and (inter)national institutions, as well as directly with local stakeholders, to root research and management in local socio-ecological context (i.e., livelihood demands and local perspectives), communicate results appropriately, and bolster informed land stewardship. In particular, ethnographic and ethnohistorical accounts are required to understand how diverse stakeholders from local communities perceive and engage with grassy biomes (e.g., Kariuki et al., 2022). Transdisciplinary engagement can improve the tools and topics used to inform ethnographic inquiries, and maximize their relevance to effective and co-beneficial land management decisions.

Harness community perspectives and establish fluid lines of communication between research, management, and stakeholders

Visual and auditory communication tools provide powerful field resources to facilitate stakeholder engagement and collaboration around grassy biome research and management (e.g., Newman et al., 2020). For example, spatial and temporal dimensions of grassy biome evolution and stewardship can be explored through collaborative mapping exchanges (Capitani et al., 2016; Dunn, 2007; Kariuki et al., 2021, 2022; Larrain & McCall, 2019; Ramirez-Gomez et al., 2015), strategy gaming workshops (Bodonirina et al., 2018; Ravaka et al., 2021; Reibelt

et al., 2021; Waeber et al., 2021), online conversation forums, virtual reality and 3D simulations (e.g., Davis et al., 2021; Fisher et al., 2019), web-accessible video clips surrounding community, conservation, and research knowledge (Colloredo-Mansfeld et al., 2020), animations (e.g., Development Corridors Partnership, 2021), posters, radio shows, podcasts, and artwork (e.g., Wang et al., 2017; Feom'bezo [voices of the Vezo] radio show). These communication tools require translation into international and local languages, and often technology and internet access. Direct involvement of local stakeholders in research is also needed, through researchers traveling to communities or delegations of community members visiting research institutions, to establish communication, brainstorm research plans, and develop communication networks among stakeholders from different regions (e.g., Vezo ecological exchange project: Douglass, Hixon, et al., 2019; Douglass, Morales, et al., 2019; Douglass, Walz, et al., 2019).

Given that stakeholders are typically diverse groups of people with different knowledge, perspectives, and opinions, ample resources and time are required to develop meaningful engagement between researchers and local communities, and to build trust and transparent, reflective communication. In addition, researchers need to strive to represent all local views fully and honestly, and avoid selectively emphasizing views that support their own. Collaboration with local land users can also improve scientific understanding of recent political, economic, and social change, and how these factors may relate to land cover changes observed with remote sensing. Funding is needed to support such communication initiatives, which can leverage impactful, long-term contributions to land management. Furthermore, providing support, training, and opportunities for local scholars can help to improve the recognition and uptake of community perspectives in research and land management (e.g., Razanatsoa, Andriantsaralaza, et al., 2021). Such measures can bolster adaptive land management decisions at multiple levels, improve the accessibility and relevance of scientific research to a broader audience, and develop best research practices and ethics (Davis et al., 2021; Schneider et al., 2020; Wilmé et al., 2016).

Open and direct lines of communication (e.g., those developed through participatory work: Douglass & Rasolondrainy, 2021; Garcia et al., 2022; Kariuki et al., 2022) are essential for supporting effective, up-to-date, and adaptive management strategies. Policy and public opinion can take long periods of time to incorporate scientific research findings, especially when messages are complex and nuanced. However, established lines of communication between researchers

and land use managers can facilitate adaptive, collaborative research actions on more reasonable timescales with appropriate stakeholders. Proactive communication campaigns with local stakeholders are desperately needed to inform scientific inquiries and to steer research toward questions of topical importance to grassy biome management.

Identify and overcome misconceptions and oversimplifications in scientific research

There is a need to expand research beyond oversimplifications of ecosystem characteristics—“natural versus anthropogenic,” “ancient versus anthropogenic,” “grassland versus woodland,” “tree versus grass,” “grazer versus browser”—toward fuller and more nuanced investigation of ecosystem diversity and function. In particular, more information is needed regarding the biodiversity and disturbance characteristics, such as fire and herbivory functional traits, for a range of C_3 and C_4 plants. This is especially important for C_3 plants that can form large components of grassy biomes (e.g., herbaceous dicots, ericoids, non-graminoid monocots such as lilies and orchids, geoxyles, C_3 grasses, and sedges; Hempson et al., 2015). Basic characterization of biodiversity and land use practices is also needed to reverse narratives that all grassy biomes are similar and of limited ecological importance, expand understanding of fire patterns and use, and promote effective biodiversity management (e.g., Haines-Young, 2009; Kull & Lehmann, 2022; Lehmann et al., 2022; Marchant, 2010; Phelps et al., 2022). Further, interdisciplinary exploration is needed to clarify how trees and shrubs occurring in grassy biomes, such as *Uapaca bojeri* (tapia), *Sarcolaena oblongifolia*, and *Faurea forficuliflora*, have evolved, or how their distribution has changed in terms of woody germination and recruitment, composition and structure, and decadal dynamics observed with remote sensing imagery. To address these knowledge gaps, more nuanced investigation of human-environment interaction is needed, which considers human modifications as part of nature, but also seeks to empirically identify regional heterogeneity and interrelationships between biodiversity and disturbance dynamics in grassy ecosystems across the globe (e.g., Burney, 1987; Lehmann et al., 2011, 2022; Phelps & Kaplan, 2017; Phelps, Broennimann et al., 2020; Phelps, Chevalier et al., 2020; Davis et al., 2024; Phelps et al., 2022; Phelps, et al., 2025b). Practical future studies will inform adaptive land management strategies by disentangling the variety of ways in which both human land use and other drivers of

environmental change modify landscapes (e.g., Razanatsoa, Virah-Sawmy, et al., 2021).

CONCLUSION

Transdisciplinary understanding of vegetation dynamics in tropical grassy biomes is urgently needed to support sustainable ecosystems and livelihoods globally. We provide a framework that offers four contributions to improving research and management of grassy biomes by focusing on Madagascar as a microcosm of the global tropics: (1) a globally common terminology reflecting ecosystem function and disturbance processes; (2) a summary of current data contributions and knowledge gaps for research on Madagascar's grassy biomes; (3) 20 Madagascar-inspired research questions to move grassy biome science and management forward; and (4) three key approaches to fostering transdisciplinary, inclusive research and management practices: improved integration of past, present, and future datasets; enhanced understanding of disturbance dynamics; and examination of degradation narratives and bolstering local perspectives. Our framework offers a foundation for grassy biome research that can support more optimal management of biodiversity, livelihoods, and ecosystem function—both on Madagascar and across the globe.

AUTHOR CONTRIBUTIONS

Manuscript conception and design was initiated by Leanne N. Phelps, Caroline E. R. Lehmann, Jan Hackel, Kristina Douglass, Dylan S. Davis, Estelle Razanatsoa, George P. Tiley, Brooke Crowley, and Maria S. Vorontsova, leading to an international, interdisciplinary workshop on July 27–30, 2021. During the workshop, coauthors participated in interactive activities to establish manuscript content. The first manuscript draft was led by workshop co-organizers following the workshop (Leanne N. Phelps, Dylan S. Davis, Jan Hackel, Estelle Razanatsoa, Tanambelo Rasolondrainy), developed with co-advisors (Caroline E. R. Lehmann, Kristina Douglass, Maria S. Vorontsova, Brooke Crowley), and revised by coauthors. Figures were developed by Leanne N. Phelps, with input from Dylan S. Davis and Jan Hackel. The second and third manuscript drafts and data compilation were led by Leanne N. Phelps and developed online among coauthors. Workshop content contributions and/or manuscript revisions were contributed by all coauthors. Author order reflects tiers, organized alphabetically: (1) lead and corresponding author, (2) co-organizer, (3) outstanding contributions, (4) core contributions, (5) supplementary contributions, (6) co-advisor.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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Data (Phelps et al., 2024) are available in Dryad: <https://doi.org/10.5061/dryad.1zcrjdg0p>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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