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Past, Present, and Future of Forbs in Old-Growth Tropical and Subtropical Grasslands

Frances Siebert,[1] Mariska te Beest,[2,3,4] Richard Fynn,[5] Jitka Klimešová,[6,7] Craig Morris,[8,9] Sindiso Nkuna,[9] Stefan Siebert,[1] and Alessandra Fidelis[10]

[1]Unit for Environmental Sciences and Management, North-West University, Potchefstroom, South Africa; email: frances.siebert@nwu.ac.za

[2]Copernicus Institute for Sustainable Development, Utrecht University, Utrecht, The Netherlands

[3]Centre for African Conservation Ecology, Nelson Mandela University, Gqeberha, South Africa

[4]Grasslands, Forests and Wetlands Node, South African Environmental Observation Network (SAEON), Pietermaritzburg, South Africa

[5]Okavango Research Institute, University of Botswana, Maun, Botswana

[6]Institute of Botany of the Czech Academy of Sciences, Třeboň, Czech Republic

[7]Department of Botany, Faculty of Science, Charles University, Prague, Czech Republic

[8]Agricultural Research Council – Animal Production Institute (ARC-API), Pietermaritzburg, South Africa

[9]School of Life Sciences, University of KwaZulu-Natal, Scottsville, Pietermaritzburg, South Africa

[10]Lab of Vegetation Ecology, Universidade Estadual Paulista (UNESP), Rio Claro, Brazil

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Abstract

Forbs are important contributors to species diversity and ecosystem functions in low-latitude grasslands, where they support diverse herbivore communities and millions of people. Native forb assemblages tolerate disturbances and physiological stressors (fire, herbivory, drought, and frost) that together have shaped their exceptional functional diversity. Yet, compared to trees and grasses, forbs have received much less attention in grassland studies until recently. Here, we review forb-centric literature to illustrate that land conversion and responsible management of fire and herbivory are crucial to maintaining forb diversity. Management practices promoting forb

diversity offer (*a*) high-quality food items and medicinal resources that support rural livelihoods and animal diversity (from wild ungulates and livestock to fossorial rodents and insects), including their adaptive foraging patterns, and (*b*) carbon and nutrient inputs that regulate belowground processes. Improved understanding of the above- and belowground regeneration strategies of forbs is critical for restoration and conservation to secure their services in future old-growth tropical and subtropical grasslands.

1. INTRODUCTION

Forbs: nongraminoid flowering plants growing in the herbaceous layer that may be completely herbaceous, or have limited aboveground lignified tissues; belowground tissue ranges from herbaceous to woody

Underground storage organ (USO): represents many different morphological types; in tropical grasslands, USO biomass can be >10 times greater than the aboveground biomass

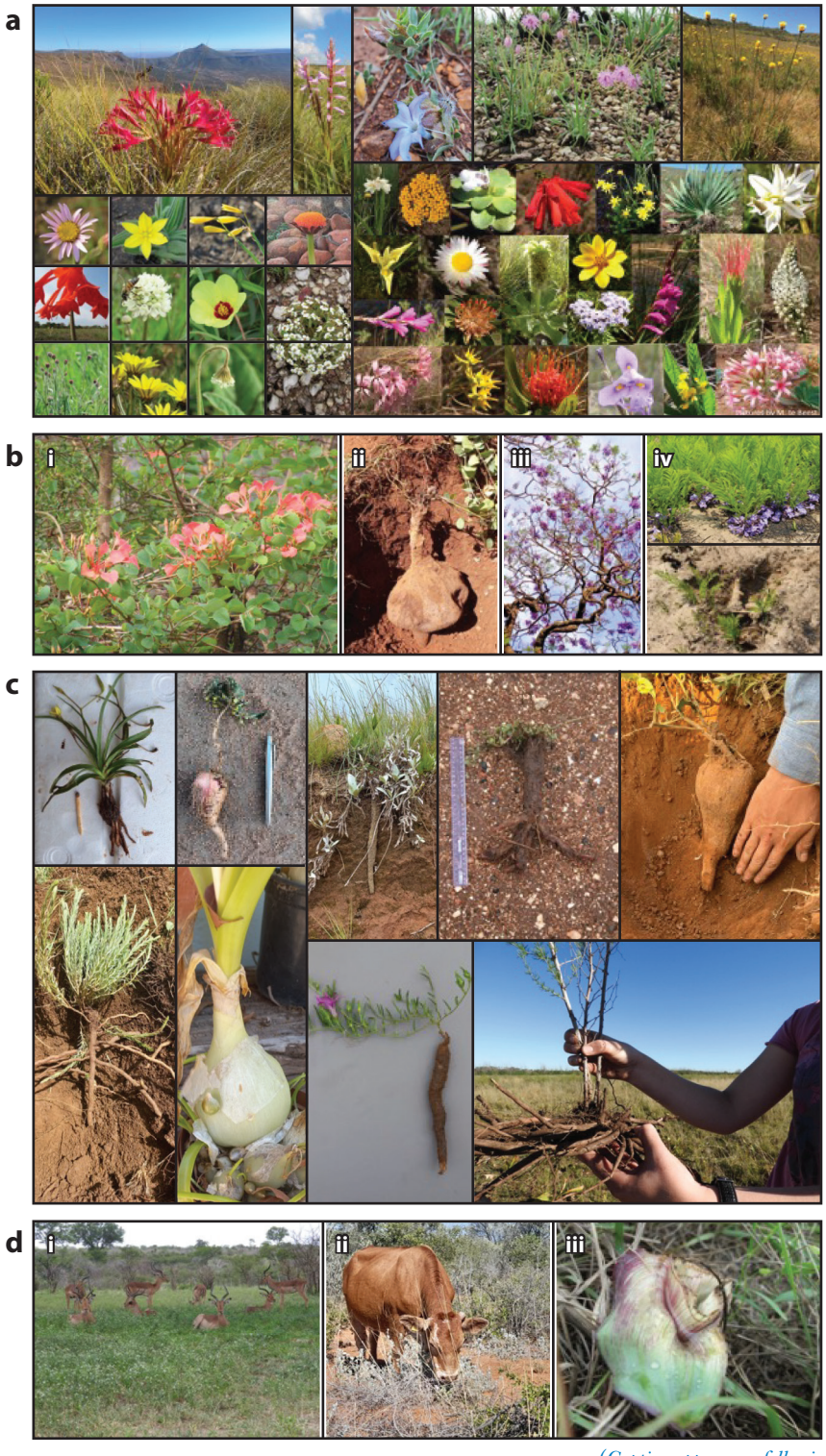
Geoxyles: herbaceous aboveground plants with large belowground woody structures; developed in high rainfall and high fire frequency ecosystems (also known as suffrutex, underground tree, subshrub)

Tropical grasslands: old-growth grasslands, savannas, and woodlands of the tropics and subtropics dominated by C_4 grasses; they contain a high diversity of long-lived perennial forbs

Ecological research is increasingly acknowledging the value of forbs as a highly diverse and ecologically dynamic plant group. However, the term forb is widely used to differentiate trees, shrubs, graminoids, ferns, and mosses from all remaining plant growth forms (Siebert & Dreber 2019). A clear functional description of forbs remains limited, and the term forb in the literature is used to represent a wide array of life forms and functional types across numerous plant families that often share phylogenetic lineages with several tree species (e.g., Fabaceae) (Maurin et al. 2014, Zhao et al. 2021) (**Figure 1**). In this review, we consider forbs to be an inclusive term for nongraminoid flowering plants that carry most of their aboveground biomass within the herbaceous layer (i.e., understory). Species in the reviewed literature include completely herbaceous plants; plants that produce lignified aboveground plant parts that are alive only during the growing season; and plants with herbaceous aboveground parts that produce lignified, or woody, underground storage organs (USOs), such as geoxyles (Maurin et al. 2014) (**Figure 1**).

Grasslands are severely impacted by agricultural expansion, climate change, invasive species, and nitrogen deposition (Bråthen et al. 2021, Stevens et al. 2022). Over 75% (12.5×10^6 km^2) of the remaining grasslands of the world are C_4 grass–dominated old-growth tropical grasslands and subtropical grasslands (**Figure 2**) (see the sidebar titled Understanding Old-Growth Tropical and Subtropical Grasslands) that have been reduced to approximately 65% of their original preindustrial extent [estimates based on Hobohm et al. (2021)]. The proportion of remaining old-growth grasslands ranges from as low as 20% in the Brazilian savanna (i.e., Cerrado) to 70% in Africa (Hobohm et al. 2021). Recent alarm calls to protect old-growth tropical and subtropical grasslands (hereafter, tropical grasslands) are premised in part on the high taxonomic, phylogenetic, and functional diversity of forbs, which account for the high levels of plant diversity and endemism in these ecosystems (Zaloumis & Bond 2011, Parr et al. 2014, Siebert & Dreber 2019, Nerlekar & Veldman 2020, Clark et al. 2022, Nerlekar et al. 2022). Nonetheless, forbs have long been neglected by researchers and land managers, especially when compared to the emphasis on graminoids and trees, which continue to be the primary focus of investigation in ecology and rangeland science in tropical grasslands (Scholes & Archer 1997, Sankaran et al. 2004, Bond 2008, Siebert & Dreber 2019, Case et al. 2020, Staver et al. 2021).

Forbs in tropical grasslands have supported people since the dawn of humankind. Millennia before the emergence of the term ecosystem services (ESs), tropical grasslands provided nature-based resources that supported human livelihoods. Despite their much lower biomass and perceived inferior role in ES delivery and ecological processes compared to grasses and trees (Siebert & Dreber 2019), forbs have served hominids with food and medicinal resources for millennia. For instance, the consumption of starchy, geophytic forbs with USOs by early hominids is key to understanding human evolution (Landen & Wrangham 2005). More recent evidence confirmed USO consumption by plant gatherers in Africa ~170,000 years ago (Wadley et al. 2020), roughly contemporaneous with the origin of modern *Homo sapiens*. Ever since,



(*Caption appears on following page*)

Figure 1 (*Figure appears on preceding page*)

(*a*) Examples of the high species diversity of tropical grassland forbs. (*b*) Their phylogenetic diversity remains unknown, but tropical grassland forbs evolved independently across plant lineages. Forbs with underground storage organs (USOs) are shown with their tree and shrub relatives. (*i*) The shrub *Bauhinia galpinii* and (*ii*) its related forb *Tylosema fassoglense* from southern Africa; (*iii*) *Jacaranda mimosifolia* and (*iv*) the geoxyle *Jacaranda decurrens* from Brazil. (*c*) Variation in the morphological modifications, structures, bud position, and size of USOs allows forbs to avoid or tolerate disturbances or extended periods of unfavorable conditions. (*d*) (*i*) Wild and (*ii*) domestic herbivores use forbs as high-quality forage resources; (*iii*) high-intensity grazing and trampling cause damage to the aboveground parts of forbs. Photographs provided by (*a–d*) Frances Siebert, (*a*) Mariska te Beest and Craig Morris, (*a* & *b*, subpanel *iv*) Alessandra Fidelis, (*d*, subpanel *ii*) Richard Fynn, and (*d*, subpanel *iii*) Sindi Chamane.

human livelihoods in tropical grasslands have been supported by forbs as a source of food and/or medicinal items for people, livestock, and game.

The long-term sustainability of the functions and services delivered by forbs, however, requires a better understanding of their role in ecological processes and how to manage tropical grassland ecosystems (Parr et al. 2014, Buisson et al. 2022, Stevens et al. 2022). Tropical grasslands evolved with and are maintained by natural disturbances such as fire and herbivory (Stevens et al. 2022). Our understanding of how these natural drivers interact to regulate tree–grass balance and other properties has steadily improved and informed grassland management (Holdo & Nippert 2023). Controlled fire and herbivory, i.e., adaptive management approaches in which climate variability and evolutionary history are accounted for (Ripley et al. 2015, Staver et al. 2021), have been

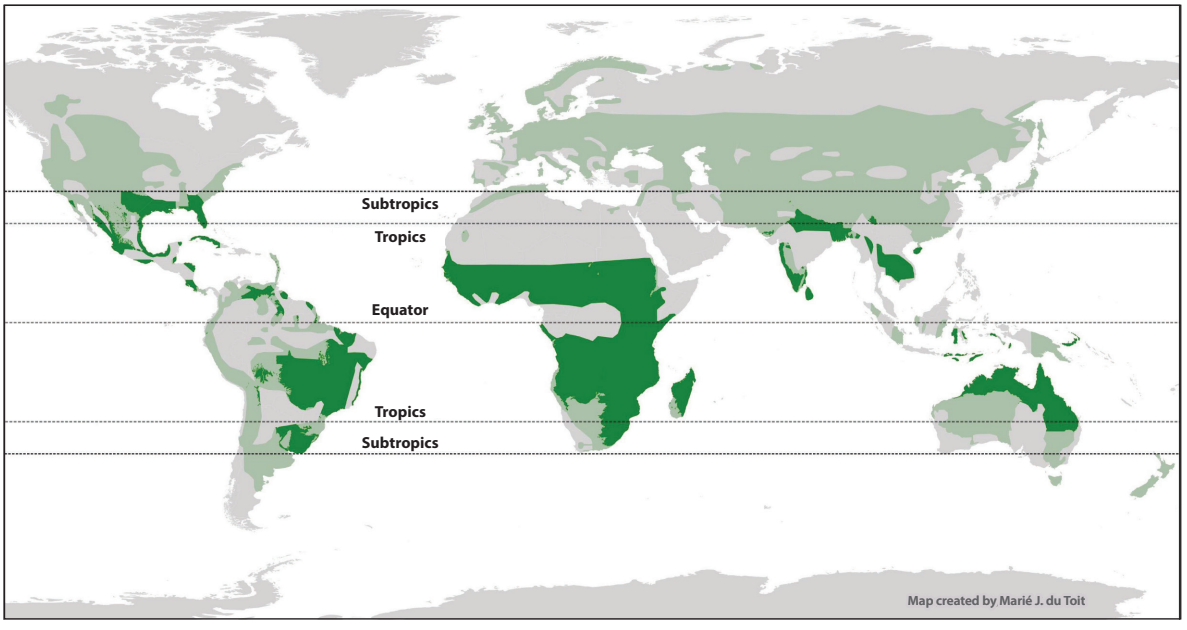


Figure 2

Grassland ecosystems of the world. Dark green areas represent the proposed extent of old-growth tropical and subtropical grasslands dominated by C_4 grasses. Areas identified as tropical or subtropical grasslands, savannas, shrublands, or woodlands (Kemp et al. 2023) with >70% cover of C_4 grasses (Osborne et al. 2014) within latitudes separating the temperate from the subtropical and tropical zones (*dark green*) were laid over the worldwide distribution of grasslands (Buisson et al. 2022) (*light green*). We acknowledge that the proposed extent of old-growth tropical and subtropical grasslands may include types that represent C_3/C_4 grass mixes, forest–grassland mosaics, temperate grasslands, and seasonally flooded grasslands at smaller scales. Map created by Marié J. du Toit.

UNDERSTANDING OLD-GROWTH TROPICAL AND SUBTROPICAL GRASSLANDS

Grasslands are broadly defined as terrestrial ecosystems with a continuous herbaceous layer dominated by grasses. Physiognomically, they include treeless grasslands, open canopy savannas, and woodlands (Veldman et al. 2015). Grasslands span from tropical and subtropical savannas to temperate grasslands and steppes (Buisson et al. 2022). Grasslands of the world consist of two distinctly different types based on their antiquity: (*a*) secondary, mostly anthropogenic grasslands that emerged in recent times (e.g., owing to deforestation or agriculture) and (*b*) old-growth grasslands that are ancient ecosystems characterized by high herbaceous diversity and endemism and long-lived perennial forbs maintained by fire and herbivory. Old-growth tropical and subtropical grasslands are distinguished from other grasslands by their geographical extent (**Figure 1**), exposure to seasonal droughts, and C_4 grass dominance. These ecosystems generate nutritious but combustible herbaceous communities that support a high diversity of animals including the world's most diverse megafauna. Old-growth tropical and subtropical grasslands may include locally temperate and montane C_4 grasslands shaped by similar ecological and evolutionary forces. Old-growth tropical and subtropical grassland forbs have developed unique strategies to survive fire, herbivory, seasonal, and episodic stress. They are functionally diverse, particularly in underground storage organ types that support repeated resprouting, long-term persistence, and coexistence with grasses and trees (**Figures 1** and **3**).

reported to reduce tree cover and accumulated unpalatable leaf litter from perennial C_4 grasses through combustion (fire) and consumption and trampling (herbivores) to support a substantial cover of palatable, perennial grasses—a common measure of pasture condition (Parr et al. 2014). However, centuries of grassland management practices designed to enhance ecosystem productivity have overshadowed the potential role of forbs in either reinforcing or reforming our current understanding of tropical grassland functioning and how these ecosystems should be managed to optimize not just production but also resilience, stability, and biodiversity.

Here, we synthesize evidence on the roles of forbs in tropical grasslands, challenging perceptions of their subordinate contribution to ecosystem functions and ES delivery in the Anthropocene. Considering that tropical grasslands are at imminent risk from land conversion, afforestation, and other anthropogenic pressures, a synthesis of our current understanding of how forbs affect long-term stability through biodiversity, resource use, and ecosystem processes is timely. In light of the increasingly well documented roles of forbs, we propose future directions for grassland management, conservation, and restoration, including a set of particularly high-priority research topics (see the Future Issues).

2. THE ORIGIN AND SIGNIFICANCE OF FORB DIVERSITY IN TROPICAL GRASSLANDS

2.1. Diversity and Endemism

The substantial contribution of forbs to total plant diversity in global grassy ecosystems is progressively being acknowledged (e.g., Bond & Parr 2010, Bråthen et al. 2021, Endress et al. 2022), although the exact proportion is yet to be quantified. Regional-scale floristic assessments of tropical grasslands reported that forbs (including geoxyles) account for over 50% of total plant species richness across continents, of which Asteraceae and Fabaceae represent the most dominant plant families across regions (**Table 1**). Accurate figures on forb species' endemicity across the full extent of tropical grasslands remain limited, since endemism studies are largely restricted to specific geographic regions, political boundaries, or geological substrates, which may extend across different ecosystem types. In Brazil, India, and South Africa, floristic studies have estimated forb

Table 1 Contribution of forb species and dominant plant families to regional species richness in several tropical grassland vegetation types

Vegetation type	Country	Forb richness (%)	Dominant forb families	Reference(s)
Montane grassland	South Africa	70	Asteraceae, Fabaceae, Malvaceae	Zaloumis & Bond 2016
Subtropical grassland	South Africa	78	Acanthaceae, Amaranthaceae, Fabaceae, Portulacaceae	Siebert & Scogings 2015
Tropical grassland	Angola	30 (Geoxyles only)	Asteraceae, Fabaceae, Lamiaceae, Rubiaceae	Meller et al. 2022
Tropical grassland	Madagascar	50	Commelinaceae, Fabaceae, Hyacinthaceae, Hypoxidaceae, Iridaceae, Orchidaceae	Bond et al. 2008
Cerrado	Brazil	40	Eriocaulaceae, Fabaceae, Orchidaceae, Xyridaceae	Rodrigues & Fidelis 2022
Tropical grassland	India	70	Acanthaceae, Asteraceae, Fabaceae, Euphorbiaceae	Nerlekar et al. 2022
Tropical grassland	Sri Lanka	70	Asteraceae, Fabaceae, Rubiaceae, Scrophulariaceae	Wijesooriya & Perera 2007
Tropical grassland	Australia	50–70	Asteraceae, Convolvulaceae, Fabaceae, Malvaceae	Kutt & Kemp 2012, Fensham et al. 2014
Subtropical grassland	Florida, USA	50	Asteraceae, Ericaceae, Xyridaceae	Orzell et al. 2024

endemism levels to be 12 to 25% of grassland floras. Most of these endemics belong to the Apocynaceae, Asteraceae, Euphorbiaceae, Fabaceae, and Lamiaceae (Iganci et al. 2011, Clark et al. 2022, Nerlekar et al. 2022).

The phylogeny of grasses (Poaceae) is well documented (Gallaher et al. 2022), whereas the phylogenetic distribution of tropical grassland forbs remains limited to lineages with USOs (Maurin et al. 2014, Howard et al. 2023). The origin, expansion, and diversification of megaherbivores (i.e., >1,000 kg) from the Oligocene to the early Miocene (roughly 16–30 Mya), in parallel with climate cooling and drying and the proliferation of fire-adapted C_4 grasslands in the late Miocene and Pliocene (roughly 3–8 Mya) (Bredenkamp et al. 2002, Bond 2008, Edwards et al. 2010), suggest diversification and paleoendemism (Ferreira & Boldrini 2011, Veldman et al. 2015) and the divergence of functionally diverse lineages of forbs across tropical grasslands (**Figure 1**).

Selective pressures associated with fire (across all tropical grasslands) (e.g., Kutt & Woinarski 2007, Bond et al. 2008, Fidelis et al. 2012, Maurin et al. 2014, Gordijn & O'Connor 2021, Rodrigues & Fidelis 2022), native herbivory (mostly in Africa) (e.g., Linstädter et al. 2014, Morris & Scott-Shaw 2019, Pansu et al. 2019), seasonality (seasonal variation) (e.g., Wijesooriya & Perera 2007, Howard et al. 2023), occasional frost events (e.g., Fynn et al. 2004, Meller et al. 2022), and drought (e.g., Fensham et al. 2014, Siebert et al. 2020, van Coller et al. 2021) explain forb diversity and their functional adaptations to optimize plant fitness through mechanisms limiting resource competition (i.e., plant growth and reproduction) and maximizing persistence (i.e., avoidance or tolerance of disturbances) (Wigley et al. 2020).

A remarkable strategy used by tropical grassland forbs is the production of complex belowground storage organs that produce adventitious buds on fleshy or lignified organs that consist of modified leaves, stems, roots, or combinations thereof (e.g., lignotubers are composed of lignified stems and roots, and bulbs of a stem with fleshy leaves) (Pausas et al. 2018) (**Figure 1**). These belowground structures (USOs) are key for the long-term persistence of both individuals and populations, as they store carbohydrate reserves and carry buds that allow for resprouting when conditions are favorable for aboveground growth (Appezzato-da-Glória et al. 2008,

Ferraro et al. 2022). Besides their function in resprouting after disturbance, some of these structures allow for clonal multiplication and lateral spread (e.g., rhizomes), permit survival through dry seasons (e.g., bulbs), or are adapted for space occupancy (e.g., lignotubers). This morphological diversity enables forbs to occupy different functional niches (Klimešová et al. 2023; Klimešová & Herben 2024).

Ruderal: having adaptive strategies enabling a plant species to be the first to colonize disturbed areas

2.2. Contribution to the Belowground Carbon Pool

Carbon estimates in tropical grasslands remain focused on the contributions of trees and grasses to the carbon pool, and although strong evidence of the importance of grasses to belowground plant and soil organic carbon (SOC) has been put forward in recent literature (e.g., Wigley et al. 2020, Zhou et al. 2023, Stevens & Bond 2024), the contribution of forb-derived carbon remains poorly quantified in tropical grasslands. Ecosystem plant carbon is commonly estimated using the widely employed conversion factor of 50% of the corresponding plant biomass (Ma et al. 2018), which is usually derived from detailed measurements of the aboveground plant parts; when belowground parts are considered, measurements are often restricted to fine roots, even in grassland studies (Bai & Cotrufo 2022). The belowground biomass in grasslands is formed not only by roots but also by USOs (Meller et al. 2022, Bombo et al. 2022) from perennial forbs that confer robustness to recurrent disturbances, seasonality, and episodic extreme events or adversities. Although total belowground plant biomass in tropical grasslands outweighs the aboveground biomass (Teixeira et al. 2022) by ratios between 2 and 20 (Mokany et al. 2006), the inclusion of belowground plant biomass and growth forms beyond trees and grasses remains neglected. Hence, the current estimation of the grassland carbon pool is likely to be underestimated (Ottaviani et al. 2024). For instance, the biomass of USOs in a Brazilian tropical grassland was estimated as 882 g/m^2, which is 1.5 times more than its aboveground biomass (Teixeira et al. 2022). The longevity of USOs, particularly woody USOs, may exceed decades (Alves et al. 2013, Dayaram et al. 2020), whereas the longevity of USOs in temperate grasslands is lower (approximately a decade), since they are less lignified (Bartušková et al. 2022), but their longevity still exceeds that of fine roots. Although belowground organs represent a large pool of carbon, we lack knowledge about their contribution to soil carbon and its different fractions [e.g., the particulate organic matter (POM) and mineral-associated organic matter (MAOM) fractions, which differ in persistence (Bai & Cotrufo 2022)]. In grassland SOC studies, it is also widely assumed that grasses explain C_4 signals and trees and shrubs explain C_3 signals from carbon stable isotope studies ($\delta^{13}C$), whereas forbs display C_3, C_4, and crassulacean acid metabolism (CAM) photosynthesis (Wigley et al. 2020). As such, tropical grassland carbon stock studies have not yet been able to differentiate (*a*) between the C_4 signals derived from ruderal C_4 forbs (e.g., Amaranthaceae) and those from C_4 grasses or (*b*) between the C_3 signals derived from trees and shrubs and signals from lignified C_3 USOs derived from perennial forbs. The main decomposers of herbaceous versus woody USOs, the time required to decompose these materials, and the ways in which decomposers contribute to soil carbon sequestration in POM versus MAOM also remain unknown. Methods to distinguish the contributions of forbs to SOC from those of grasses or trees and shrubs and more studies on the ecology of USOs, their longevity, and their role in belowground soil processes are crucial to develop a deeper understanding of carbon sequestration in tropical grasslands.

2.3. Forbs and Plant Community Dynamics

2.3.1. Coexistence with other growth forms. The nature of coexistence between trees and grasses in tropical grasslands has been an intensive focus of research for decades (Scholes & Archer 1997, Sankaran et al. 2004, Bond 2008, Staver et al. 2021, Biro et al. 2024). Detailed investigation

of the intricate relationship between these two major growth forms (based on >1,000 literature sources published since 2000, obtained from Google Scholar on March 30, 2024, using the search string "tree-grass coexistence AND savanna AND grassland") has improved our understanding of the mechanisms responsible for a continuous herbaceous layer and a discontinuous stratum of shrubs and trees (Sankaran et al. 2004). Herbaceous plants other than grasses and lignified plants other than shrubs and trees have, however, received much less attention in studies assessing competition and facilitation with the aim of understanding the causes and directions of changes in coexisting growth forms in tropical grasslands (Siebert & Dreber 2019, Coverdale et al. 2021, Holdo & Nippert 2023).

Relative to trees, shrubs, and grasses, many forb species in nutrient-limited ecosystems are more efficient at nutrient acquisition where soil nutrients are locally high and heterogeneously distributed (Ludwig et al. 2004), and they often dominate over grasses in subcanopy habitats where soil moisture is higher and light lower (Belsky et al. 1993). When grass biomass, and hence competition for light resources, is significantly reduced by intensive livestock grazing and/or trampling, forbs may dominate over grasses (Linstädter et al. 2014, Augustine et al. 2019), although such dominance is specific to the species and functional group, e.g., prostrate-growing and perennial species that bear their buds at or below the soil surface (Morris & Scott-Shaw 2019). Other explanations for forb dominance over grasses include belowground resource use, as the fibrous roots of grasses typically reach up to 30 cm of the soil profile, while certain forb species have rooting depths >30 cm to escape competition. Forb species with USOs may also have a competitive advantage over grasses during dry conditions (Nippert & Knapp 2007, Wilcox et al. 2023) (**Figure 1**). Palatable perennial forbs and grasses can also be codominant, as was reported in a grazed, nutrient-rich semiarid subtropical grassland during years with normal to below-average rainfall (van Coller et al. 2018). Given our limited understanding of long-lived perennial forbs with USOs (Section 2.2) and the overall neglect of the role of forbs in understanding resource distribution in grasslands, more studies on the coexistence mechanisms of multiple plant functional types beyond trees and grasses are needed for a biologically inclusive account of tropical grasslands and their functions, which will improve forecasts of tropical grassland responses to future climate scenarios (Holdo & Nippert 2023, Wilcox et al. 2023).

2.3.2. Forbs and fire. Tropical grassland forbs are less combustible than grasses due to their higher water content (Zanzarini et al. 2022). Although they produce lower aboveground biomass compared to grasses (Siebert et al. 2020), they are consumed by fire since their aboveground parts are mostly trapped within the grass layer. For forbs to persist during or after fire events, they need to have (*a*) a viable seed bank, from which the seeds must be able to germinate after fire, and/or (*b*) a viable belowground bud bank, located on storage organs that can rapidly allocate resources to replenish aboveground biomass. In tropical savannas there is a high percentage of empty (e.g., Orobanchaceae), nonviable (e.g., Apiaceae), and dormant seeds (e.g., Fabaceae) (Dayrell et al. 2017). Moreover, seeds with physical dormancy usually do not have their dormancy broken by heat shock (Ordóñez-Parra et al. 2023), which suggests that seed banks likely play a minor role in postfire regeneration compared to bud banks. Fire-prone tropical grasslands therefore support a high diversity of belowground bud-bearing USOs that often consist of woody structures bearing numerous buds, including xylopodia (shoot bases and a main root), lignotubers (belowground woody organs with a tuberous root), and rhizomes (both woody and nonwoody belowground rooting stems). The diversity of these resprouting organs with their numerous buds is key to stabilizing herbaceous cover in postfire environments (Fidelis et al. 2012, Rodrigues & Fidelis 2022). When fire is excluded, forbs are the first group to show decreases in aboveground (Overbeck & Pfadenhauer 2007, Rodrigues & Fidelis 2022) and belowground biomass, with

lower bud bank density and numbers of belowground organs (Fidelis et al. 2014, Bombo et al. 2022), as they are overgrown by other species. Although it is well documented that grasses are well adapted to fire in tropical grasslands (Archibald et al. 2019), forbs in fire-prone ecosystems are comparatively resistant to fire at the individual level and are more susceptible to population declines in the absence of fire. How long these species can persist in communities where they rely on the next opportunity (e.g., fire event) to resprout from belowground structures is unclear.

Another outstanding adaptation to fire is the capacity of certain forb species to flower rapidly after fire [bloomers sensu Pilon et al. (2021)]. In the Cerrado, many forb species exhibit flowering peaks at 15 (Zirondi et al. 2021) to 30 (Fidelis & Blanco 2014) days after fire. In a review of the Cerrado, Fidelis & Zirondi (2021) found that 48% of species flowering after fire were forbs, which exhibit both fire-dependent and fire-stimulated postfire flowering. This strategy ensures safe reproduction in fire-prone grasslands, as recently burned areas are unlikely to burn twice in rapid succession.

The above examples of strategies and adaptations differentiate tropical forbs from those in most temperate grasslands, where forbs rarely produce woody USOs and where resprouting primarily occurs in spring, after seasonal dormancy (Ferraro et al. 2022).

2.4. The Importance of Forbs to Invertebrates

Invertebrates in tropical grasslands are heavily dependent upon forbs as food sources and habitat. Forb species declines, due to habitat loss, have large implications for invertebrate pollinators globally, as forbs account for most animal-pollinated flower species, as opposed to grasses that are predominantly wind pollinated (Potts et al. 2010). A high diversity of arthropods is especially associated with high forb richness in the Asteraceae, Apiaceae, and Fabaceae (Botha et al. 2017). Forb species richness is therefore important for maintaining arthropod diversity in grasslands and vice versa (Stein et al. 2010), as these associations are specialized (Oleques et al. 2019). Loss of forb species is expected to have a cascading effect on higher trophic levels involving insects (Woodcock et al. 2009). For instance, in croplands surrounded by untransformed tropical grasslands in Africa, where high forb diversity supports insect refuges, predatory insects were more abundant, suggesting the possibility of lower pesticide use and greater economic benefits due to reduced pest control (Botha et al. 2018).

Grassland forbs are also important in supporting invertebrates with complex life cycles. For instance, many tropical butterfly species require a specific larval host plant (Forister et al. 2015). Ovipositing females target specific plant species, mostly forbs that are suitable forage for larvae, while pupae may be tended by ants living in the surrounding grassland and adult butterflies feed on the nectar of (and pollinate) the same species (Mega et al. 2020). These relationships are often mediated by other species endemic to tropical grasslands. For example, butterfly host-plant populations from an African grassland system have proven to be delicately maintained by megaherbivores that regulate vegetation structure (Pryke et al. 2016), whereas a study in semi-arid Kenya found that browsing ungulates tend to simplify plant–pollinator networks by reducing floral abundance (Guy et al. 2021).

Forbs can also provide ecological disservices in their interactions with insects. Some forbs may act as refuges for pest species (Moolman et al. 2014) or reduce habitat for spiders and other predatory arthropods by displacing grasses (Botha et al. 2017). As these examples show, forbs interact with their context in ways that can either enhance or limit the abundance and diversity of invertebrates, including both beneficial and pest species. Managing for specific plant genera or families may benefit specific arthropod groups at the expense of others; therefore, detailed knowledge of species-interaction networks may be required to achieve desired outcomes (Skaldina 2020).

2.5. The Importance of Forbs to Mammalian Herbivores

2.5.1. Forbs as forage. On average, tropical grassland forbs are characterized by higher nutritional quality compared to cooccurring grasses and trees, making them a valuable food source. For example, forbs in eastern African savannas are elevated in digestibility, crude and digestible protein, calcium, potassium, magnesium, and other nutrients, relative to grasses and trees (Boutton et al. 1988, Potter et al. 2022, Anderson et al. 2024). Accordingly, forbs constitute a substantial fraction of the nutritional intake of many large herbivores in grasslands worldwide. Examples of herbivores that use forbs as high-quality forage resources include antelopes such as eland, gray rhebuck, oribi, steenbok, impala, kudu, and Thomson's gazelle (Rowe-Rowe 1983, Owen-Smith & Cooper 1989, Watson & Owen-Smith 2000, du Toit 2003, Anderson et al. 2024); megaherbivores such as African elephant, hippopotamus, and rhinoceros (Landman et al. 2013); and even many species widely considered to be grass specialists, such as African buffalo and wildebeest (Pansu et al. 2022). Browsing is often used to signify the consumption of woody plants, and grazing that of grasses, yet nearly all large herbivores supplementally eat forbs (Kartzinel et al. 2015, Pansu et al. 2022), and some species rely predominantly on forbs in some seasons. Just as forbs have been overlooked relative to grasses and trees in plant ecology, they have been widely underestimated as forage in animal ecology.

Late Pleistocene extinctions have left tropical grasslands on most continents with a depauperate diversity of large herbivores, although consumption of forbs by the remaining native herbivores has been recorded for kangaroos and wallaroos in Australia (Kutt & Woinarski 2007, Reid et al. 2023), Asian elephants in Sri Lanka (Alahakoon et al. 2014), and Patagonian mara in the Cerrado (Jaksic 2023). Domestic livestock such as goats, sheep, and cattle have replaced native herbivores in tropical grasslands where megafauna became extinct (e.g., North and South America, Australia) or have been displaced by humans (e.g., large parts of Africa and Asia). Domestic herbivores are heavily reliant on forbs as nutritious food items across tropical grassland ecosystems (Kutt & Woinarski 2007, Odadi et al. 2013, Mellado et al. 2017, Müller et al. 2019, Reid et al. 2023). The high nutrient content and availability of grassland forbs, especially but not exclusively nitrogen-fixing legumes (Fabaceae), highlight their ecological significance and importance to human livelihoods (Krätli & Schareika 2010, Müller et al. 2019).

Despite their generally high nutritive value, forbs also produce antinutritional secondary compounds such as tannins, along with a variety of often highly toxic chemicals, which can deter herbivory (van Wyk & van Staden 2002). These compounds serve as defense mechanisms against both insect and mammalian herbivores, along with microbial and fungal pathogens, either by causing harm when ingested or by inducing aversion responses (Laycock 1978). Herbivores, in turn, have evolved strategies to identify and avoid potentially harmful plants or to detoxify the toxins they contain. This complex interplay between forbs and herbivores has ecological implications, influencing herbivore foraging behavior and the spatiotemporal distribution of forbs. Understanding how nutritive value interacts with the deterrent, toxic, and medicinal effects of secondary compounds is essential for comprehending the relationships between forbs and herbivores and their impact on ecosystem dynamics (Laycock 1978).

2.5.2. Foraging patterns on forbs. Large herbivores depend on diverse resources to adapt to ecological challenges throughout the year, including parasites, seasonal forage variations, and increased nutritional demands for growth and reproduction (Owen-Smith & Cooper 1989, Fynn & Provenza 2023). There are at least two key areas where forbs play critical roles in the foraging ecology of large herbivores, namely providing (*a*) high-quality forage promoting survival, growth, and reproduction and (*b*) phytochemical diversity to promote health. While grasses contain phytochemicals, eudicots offer a far wider array, which may be consumed in trace quantities due to

their potential toxicity yet still confer health benefits—for example, by regulating parasite load or gut-microbiome composition (Fynn & Provenza 2023). The functions and mechanisms of animal self-medication are likely diverse and remain almost entirely unknown.

While forbs play a key role in providing high-quality forage at certain times of the year, their specific contribution to forage reserves, bridging resources, and buffer resources during the dry season remains less clear and requires further research. Forbs are important reserve resources in areas containing deeper-rooted forbs, which remain green in the dry season (Owen-Smith & Cooper 1989). Perennial forbs with nutrient-rich USOs are also important forage resources for fossorial rodents and other digging mammals (de Villiers 1993). While consuming belowground plant parts, they locally perturb soils and boost nutrient cycling (Andersen 1987), although more research is needed to fully understand the interactions between these animals and tropical grassland forb diversity and ecological processes.

Many smaller herbaceous forbs contribute to dry-season forage reserves and buffer resources only in higher rainfall years when they persist longer into the dry season (du Toit 2003). In addition, flushes of herbaceous forbs before the first rains are consumed as a higher-quality bridging resource (Owen-Smith & Cooper 1989). Variations in forb intake across seasons, ecosystems, and local-scale nutrient hot spots (Siebert & Scogings 2015) suggest a nuanced relationship between herbivore species and these forage types (Watson & Owen-Smith 2000), which may be determined by an interaction between body size and mouth anatomy that affects the intake of forbs by different large herbivores (Fynn & Provenza 2023).

Forage reserve: dry-season forage providing adequate quality to maintain body condition over the dry season

Bridging resource: dry-season forage providing relatively high-quality green forage over the dry season

Buffer resource: low-quality resource, often the last remaining available forage that prevents mortality during drought years (key resource)

2.6. Forbs and Their Service to Human Livelihoods

Forb species constitute a large proportion of plants that offer direct benefits to humans. They are rarely used in bulk, and their ethnobotanical use and medicinal properties are often taxon specific (van Wyk & van Staden 2002), with some exceptions at functional group levels, e.g., legumes that provide nutritious forage sources for livestock (Odadi et al. 2013) and long-lived perennial forbs with large USOs that are essential in the regulation of organic carbon in the soil (Zaloumis & Bond 2016).

Grassland forbs are commonly used as food and medicinal plants by people, especially in rural parts of developing countries that are isolated from commercial markets and long-distance trade (Shackleton et al. 1998). Useful forb species may also deliver a potential source of income for rural households. In these areas, wild-growing forbs supply carbohydrates, vitamins, amino acids, and other nutrients that are essential for human health and often unavailable from other sources (Ntuli 2019), particularly during droughts, when rural communities become more dependent on natural resources that are adapted to water stress (Siebert et al. 2020). For instance, human consumption of indigenous forbs in a rural semiarid savanna was reported to be twice that of common vegetable crops (Shackleton et al. 1998). Use of indigenous forbs over exotic cultivars has further advantages, as many indigenous forbs are rich sources of dietary fiber (Ntuli 2019).

Rural communities throughout the tropics rely on traditional plant medicines, which are also traded at local and regional markets for important income, despite the growing availability of western medicine (Dubey et al. 2004). In sub-Saharan Africa, up to 94% of people in semiurban settlements use traditional medicine (James et al. 2018). In South Africa alone, an estimated 27 million people use traditional medicine, an enterprise that plays a critical role in empowering rural women (Mander 1998). Over 1,000 indigenous forb species are used medicinally in South Africa (Twilley et al. 2020), of which a large proportion is restricted to grassy ecosystems (e.g., Mander 1998). In South Africa, forbs are traded mostly in the form of their belowground organs, roots, bulbs, and tubers (66%), followed by whole-plant harvests (24%) and stems and leaves

(10%) (Mander 1998). South Asian and South American tropical grasslands also host a substantial richness of medicinal plants with USOs, of which the bulbs, corms, and tubers are harvested for medicinal purposes (Patel 2015). The majority of these harvests are destructive, and because little or no cultivation of these species occurs, harvests are derived merely from wild populations and potentially represent a threat to population persistence and diversity maintenance.

3. HUMAN-INDUCED THREATS TO FORBS

3.1. Land Conversion and Alien Plant Invasion

Expansion of land conversion for cropping, pasture, and silviculture poses the most significant threat to tropical grasslands (Parr et al. 2014, Stevens et al. 2022). An estimated 46% of the Cerrado has been converted to agriculture at a rate almost double that for the Amazon (Strassburg et al. 2017). Soil disturbance, particularly deep ploughing, damages or destroys forb USOs, roots, and bud banks (Buisson et al. 2022), which severely impacts forb diversity, endemism (Muller et al. 2021), and community composition (Nerlekar et al. 2024a). Repeated cultivation and nutrient input favor annual ruderal species over long-lived forbs (Botha et al. 2017). Even a single till reduces the persistence of perennial forbs and can substantially and irreversibly alter species composition and vegetation structure, with effects that can reverberate across trophic levels and reduce ecosystem functionality and resilience (Veldman et al. 2015, Nerlekar et al. 2024a, Slooten et al. 2023).

Mining and urbanization lead to extensive land transformation in tropical grasslands and are predicted to expand greatly in developing countries that host unexploited mineral and coal reserves. In South Africa, 63% of unprotected grassland has received applications for mineral prospecting rights (Olivier 2020). Increased mining and urbanization in tropical grasslands are predicted to have a significant impact on native forb species, as reported forb species losses after transformation were over 50% (du Toit et al. 2021, Muller et al. 2021).

Besides direct effects through soil destruction and habitat loss, mining, urbanization, and road construction also promote the introduction and proliferation of invasive alien plant species at the cost of indigenous, long-lived, perennial forbs. These invasions are a major threat to forb diversity, as they alter natural disturbance regimes. For example, invasion of paleotropical grasslands and savannas by the neotropical shrub *Chromolaena odorata* can variously limit access to grazing (Rozen-Rechels et al. 2017), reduce fire frequency while increasing fire intensity (te Beest et al. 2012), change the microclimate, and shade out shade-intolerant forb species (te Beest et al. 2015). Grasses also benefit greatly from anthropogenic effects. Owing to their fast growth, they shade native forbs and increase fire intensity, which lead to forb diversity declines (Brooks et al. 2010). For example, invasive grasses led to a decrease in forb diversity and cover in subtropical grasslands in South America (Damasceno et al. 2018, Dresseno et al. 2018). Forb diversity losses through alien invasion are similar to the negative effects caused by afforestation in tropical grasslands (Bremer & Farley 2010, Nerlekar et al. 2024a).

Commercial silviculture of exotic species and large-scale tree plantings for carbon offsets (Aguirre-Gutiérrez et al. 2023) result in complete transformation from ancient and diverse native communities to monocultures with completely transformed soils. Forb diversity in such plantations is low, and if any understory vegetation remains, the functional composition is reduced and homogenized, as shade-tolerant exotics overshade open-adapted native species (Bremer & Farley 2010, Muller et al. 2021, Nerlekar et al. 2024a). Zaloumis & Bond (2016) found a 70% decline in forb diversity in grasslands restored after afforestation. Geoxyles disappeared completely in these secondary grasslands, even though some sites had been recovering for 40 years. Furthermore, several exotic tree species used in commercial forestry and afforestation, e.g., *Pinus* spp. and *Eucalyptus* spp., have become major invaders of tropical grasslands. This problem has

increased significantly in recent years with intensifying afforestation and changes in land use (Aguirre-Gutiérrez et al. 2023).

3.2. Herbivory and Mowing

Geophytism: state of having developed into a geophyte, a herbaceous plant producing buds for new growth on belowground structures

While tropical grassland forbs have developed functional adaptations and life-history strategies to cope with stressors and disturbances (**Figure 3**; see also Section 2.3), they remain vulnerable to intensive grazing during the growing season. Repeated defoliation by herbivores can lead to a significant decrease in the size of USOs and hinder subsequent regrowth (Morris 2021a). Continuous herbivory on perennial forbs during the growing season may eventually deplete stored reserves and reduce the bud banks necessary for clonal expansion (Bartušková et al. 2022), leading to population decline or extirpation (Scott-Shaw & Morris 2015).

Similarly, while light to moderate grazing can help maintain forb diversity in tropical grasslands, overgrazing by livestock has the potential to alter species composition (Chamane et al. 2017a) and markedly reduce species diversity (Scott-Shaw & Morris 2015). Only a few prostrate short forbs whose growing points evade defoliation persist in areas subjected to recurrent, intense grazing (Siebert et al. 2020). Herbivores can also mechanically damage or remove leaves, stems, and flowers of forbs through the trampling and tearing of their hooves. Few forbs (<10%) escape damage by trampling and grazing in intensive stocking rangelands (Chamane et al. 2017b). Herbivory can also indirectly affect forbs, positively and negatively, by modifying competitive interactions. For example, nutrient redistribution in herbivore dung and urine can favor grasses (Morris 2021b), while grazing can alleviate competition for light and improve the microclimate for forb growth (Chamane et al. 2019).

The sensitivity of tropical grassland forbs to recurrent, intensive herbivory may seem counterintuitive, given that USOs and regeneration buds are protected underground (**Figure 1**). However, geophytism evolved independently in multiple monocot and eudicot lineages before the emergence of large herds of ungulates and expansion of C_4 grasslands during the Late Miocene and Pliocene (Edwards et al. 2010). Increased aridity and more pronounced seasonality, starting in the Eocene and especially during the Oligocene and Miocene, favored resprouting perennial forbs that could endure periodic resource scarcity and loss of aboveground growth through drought, fire, and frost (Pausas et al. 2018, Howard et al. 2020).

The response of forbs to herbivores is typically inferred from observed changes in plant species diversity under natural or experimentally imposed gradients in grazing, but the mechanisms underlying the response of forbs to herbivory across different herbivore guilds are not yet fully understood (Siebert et al. 2021).

Mowing for hay is a relatively benign, nonselective land use compared to cultivation, although it is not common in tropical grasslands where biomass is generally maintained by grazing. A study in South Africa reported that a single summer mow had minimal long-term effects on forb abundance and diversity, whereas double mowing reduced the abundance and diversity of forbs, especially of erect species (Fynn et al. 2004, 2005). Based on evidence from intense summer grazing effects, mowing during the growing season is expected to deplete the underground energy reserves of forbs. Effects of mowing on forbs in tropical grasslands may therefore differ from temperate regions, where annual mowing during the growing season has been shown to enhance diversity in seminatural grasslands (Hobohm et al. 2021, Eskelinen et al. 2022).

3.3. Climate-Change Effects

Grasslands are expected to be fairly resilient to climate variability due to their inherent seasonality and regular disturbances. Still, extreme droughts and deluges, more or less frequent flooding,

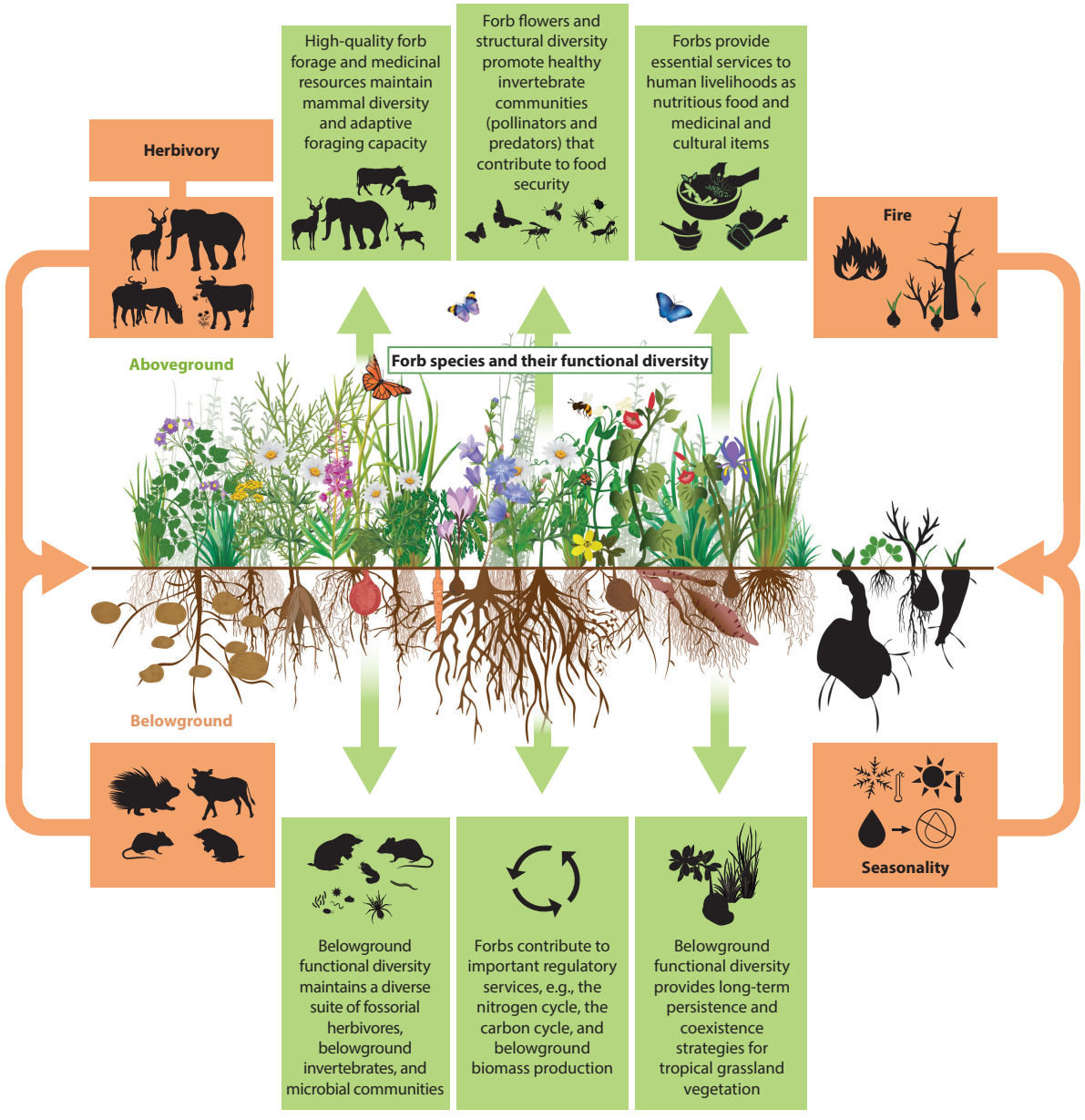


Figure 3

High species and functional diversity of forbs in old-growth tropical and subtropical grasslands reflect past selection pressures from mammalian herbivory, fire, and seasonality (*orange boxes*). Management of disturbance (herbivory and fire) is important to maintain forb diversity. In return, forb diversity provides valuable ecosystem services and functions (*green boxes*). An improved understanding of the role of belowground functional diversity of forbs is needed, especially to improve predictions of climate-change effects on the resilience of old-growth tropical and subtropical grasslands. Illustration created by Clarissa Coetzee using icons designed by Clarissa Coetzee, Pixabay, and Freepik.

unseasonal temperature extremes, and altered fire regimes due to global warming may all have severe impacts on forb communities. As most forb species use the C_3 photosynthetic pathway, they are likely to respond more strongly to elevated CO_2 (eCO_2) than C_4 graminoids because they can combine faster growth with more robust, resource-conservative leaves under higher CO_2 (Temme et al. 2017). Several forb species, however, use the C_4 pathway, including ~40% of the world's >2,000 species of Amaranthaceae, a globally distributed, forb-dominated family (Berasategui et al. 2023), and are likely to respond differently to eCO_2. When eCO_2 is combined with higher growing-season temperatures and reduced moisture availability, C_4 plants may be favored (Ripley et al. 2022). Yet, tropical grassland forbs are poorly represented in climate-modelling efforts, and studies rarely report or account for the potential influence of photosynthetic pathway on growth response or species distributions (Scheiter et al. 2024).

Resurrection plants: desiccation tolerant plants with the ability to survive in a dried-out state (4–13% relative water content) for several months

Climate models predict increases in the frequency, intensity, and/or duration of drought in many tropical grasslands, which are expected to reduce plant productivity, increase the mortality of drought-sensitive species, and shift plant community structure and functional-trait composition (van Coller et al. 2021). Tropical grassland forbs have various strategies and functional adaptations to avoid or tolerate drought, conferring some insurance against the projected impacts of drought—especially in diverse communities with high niche complementarity (Siebert et al. 2020, van Coller et al. 2021). For instance, annual and short-lived perennial forbs survive drought periods as seeds and may even take advantage of drought conditions due to reduced competition with grasses (O'Connor & Roux 1995). Long-lived perennial forbs can either remain dormant during a drought (e.g., certain bulbous species) or survive using stored reserves in their USOs from which they resprout after the drought, while others have deep perennial main roots to gain access to deep water resources. Resurrection plants can dry out completely but regain their functions when water becomes available again. Forb communities dominated by long-lived perennials can consequently recover to predrought productivity levels faster than grasses, which are more dependent on surface water (Nippert & Knapp 2007, Siebert et al. 2020). Maintaining the diversity and abundance of long-lived perennial forbs is therefore pivotal in enhancing the ecosystem resilience of tropical grasslands.

4. FORBS FOR FUTURE ECOSYSTEMS

Considering the important ecological roles of forbs and the threats they face in tropical grasslands, we propose certain management and restoration practices to safeguard the long-term ecological functioning of forbs and, hence, the integrity of tropical and subtropical open ecosystems.

4.1. Tropical Grassland Management in Favor of Forbs

The challenge to conceptualizing grassland management in favor of forbs is to establish a clear understanding of their responses to natural and anthropogenic disturbances, since the intensity, timing, and frequency of these events may impose variable outcomes for native forb communities.

4.1.1. Grazing management. Grazing-management systems are primarily aimed at meeting livestock-production objectives, but grasslands are being increasingly pressed globally to deliver a wide range of ESs, including the plant species diversity conferred by forbs (Bengtsson et al. 2019). Future intensification of grazing through increased stocking rates and densities (Jaurena et al. 2021) is likely to threaten the persistence of forbs in tropical grasslands (Section 3.2) if not implemented through a strategic, adaptive-management approach.

Adaptive-management principles developed for sustainable livestock production in tropical grasslands (Kirkman et al. 2023) can apply to the management of forbs. Moderate grazing levels are generally recommended for rangeland production and overall biodiversity preservation

(Morris 2021a). Chronic intense grazing reduces the vigor and abundance of forbs (Section 3.2) and hence affects pollinator diversity and activity if grazed areas are not afforded sufficient rest, especially during peak flowering when pollinators are most abundant. Regularly resting heavily grazed grassland for at least a full growing season (Kirkman et al. 2023) is essential to allow forbs to grow, bloom, reproduce, and, importantly, replenish their reserves in USOs and build bud banks (Morris 2021b). Understanding the duration and frequency of rest periods necessary to conserve forb and pollinator diversity is essential, although such studies are limited in tropical systems. Changes in the abundance of indicator forbs that are responsive to grazing or mowing can signal broader shifts in community composition and diversity (Morris & Scott-Shaw 2019). The establishment of indicator forbs for tropical grasslands is still nascent compared to temperate grasslands (Herben et al. 2016). Monitoring grassland condition and forb populations and adjusting grazing practices to meet strategic goals for tropical grassland conservation are therefore essential.

4.1.2. Fire management. Management of forbs through fire entails careful consideration of the burning season, frequency, and need for environmental heterogeneity to support biodiversity. Exclusion of fire may lead to a shift in forb species composition toward dominance of shade-tolerant species, while the presence or absence of disturbance, rather than its nature and timing, determines forb composition (Fynn et al. 2004, Rodrigues & Fidelis 2022). Forbs with well-developed roots and USOs are more common in fire-prone sites, and their bud bank is maintained by frequent fires (Fidelis et al. 2014, Bombo et al. 2022). Therefore, a spatiotemporally heterogeneous burning regime that includes variable burning frequencies, from frequent dormant-season burning to longer fire-return intervals, is essential for maximizing forb diversity (Fynn et al. 2005, Gordijn et al. 2018). Burning during the growing season is discouraged, as it reduces grass abundance and herbaceous cover, favoring a few forb species (Morris 2021a). In some tropical savannas, e.g., the Cerrado, frequent fires maintain forb species diversity, even during the dry season (Rodrigues & Fidelis 2022), through rapid postfire flowering strategies (Zirondi et al. 2021). The response of forb species to fire varies, and spatial environmental variability plays a crucial role in forb species composition (Uys et al. 2004). Therefore, a flexible patch-mosaic burning strategy is recommended to promote environmental heterogeneity and biodiversity while considering grazing pressure and resting periods (Gordijn & O'Connor 2021).

Fire plays a crucial role in the life cycle of many forbs, stimulating their resprouting and flowering in spring or just after fire, allowing them to access high light conditions, grow, flower, and set seed before being shaded by grasses (Lamont & Downes 2011). When fire is not a feasible management option, mowing can aid in restoring forbs in degraded grasslands by reducing grass competition for space and light. However, mowing may not have the same effect on the maintenance of forb diversity and cover as fire (Fidelis et al. 2012). Thus, in fire-prone grasslands, controlled burning is a crucial tool for forb diversity maintenance.

4.1.3. Urban green space management. Management of indigenous forbs (native flowers) in urban landscapes, including gardens, parks, and other open areas, has gained attention during the past decade. Management approaches vary and may include interventions such as mowing (Entsminger et al. 2017), fire (Carbutt & Kirkman 2022), and grazing (Gornish & Ambrozio dos Santos 2016) to maintain the richness and (re)productivity of native forbs in urban green spaces. Even when land-use change leads to forb species losses, the remaining forb species provide ecosystem resilience to the anthropogenic ecosystem through functional redundancy (Siebert et al. 2021). Management of forbs in urban areas is crucial, as they provide valuable ESs, such as forage and habitat for invertebrates. A valuable contribution of forbs across urban and periurban landscapes is to provide agricultural food security through the maintenance of vigorous pollinator communities (Ganser et al. 2018). Native forbs are becoming more tolerated in urban

environments beyond provisioning and regulating services, and people are increasingly accepting a messier ecological aesthetic that includes wildflowers instead of the norm, which relies on manicured lawns of exotic grass species (Hoyle et al. 2017). For instance, native forb species became key to urban greening in recent years through restoration efforts worldwide and have been maintained through active transplants (Hitchmough 2009), seeding (Schröder & Kiehl 2020), and preservation of fragmented natural stands (van der Walt et al. 2015). There is a growing recognition that forbs are not just weeds but have their part to play in human well-being. This is witnessed by people's gardening habits (and municipal policy), which are shifting toward a more thoughtful and deliberate approach to maintaining indigenous forb diversity and its associated ESs (Cilliers et al. 2018).

4.2. Conservation

The diversity of forbs and their important role in ES delivery are repeatedly invoked as motivations for grassland conservation and restoration (e.g., Veldman et al. 2015, Bråthen et al. 2021, Buisson et al. 2022). Yet, grassy ecosystems are still declining due to global climate change, land conversion, and poor management of the ecological processes that regulate their integrity (Stevens et al. 2022). Conservation areas in tropical grasslands remain limited to reserves and national parks. The inclusion of smaller reserves in conservation planning has benefitted forb conservation in tropical grasslands that are fragmented by land conversion (Smith et al. 2006). Smaller reserves successfully protect endemic and/or vulnerable forb species, such as the high diversity of perennial forb species that are being protected inside wildflower reserves (e.g., Lubke & Judd 1994, Johnson & Curry 2017). To effectively conserve biodiversity and secure ES delivery, smaller reserves and fragments of untransformed areas should be included in future conservation planning (Volenec & Dobson 2020). However, the conservation of forb diversity cannot rely solely on formal protection in reserves. A collaborative, transdisciplinary, and public-engaging approach is needed to develop an awareness among the millions of people who, knowingly or unknowingly, rely on or value the functions and services provided by forbs in tropical grasslands.

4.3. Restoration

Restoring secondary grasslands after cropland abandonment or clear-cutting of plantations poses significant challenges (Slooten et al. 2023, Nerlekar et al. 2024a) and in some cases may be impossible; disturbed tropical grasslands can take centuries or millennia to regain richness in perennial forbs (Zaloumis & Bond 2011, Nerlekar & Veldman 2020, Nerlekar et al. 2024a). Land conversion and degradation of the remaining tropical grasslands should therefore be avoided where possible. Although grasses are valuable for establishing vegetation cover during restoration practices and acting as nurse plants in harsh environments (Ntloko et al. 2022), restoration of tropical grasslands using forb species remains limited (Nerlekar et al. 2024b). Reasons for restoration seed mixes being poor in forb species include localized distribution of populations, seed morphology restrictions for storage (e.g., recalcitrant species), and species-specific dormancy-breaking requirements, which limit seed availability (Buisson et al. 2021). Trait-based approaches to restore forbs have therefore been suggested to address community reassembly (Silveira et al. 2020). Passive restoration involves reintroducing a limited number of species (Pilon et al. 2023), while active methods like reseeding, planting, or topsoil translocation are more effective for diverse forb recovery (Gibson-Roy 2022, Giles et al. 2022, Gerrits et al. 2023). Large-scale active restoration is costly, however, and may not fully restore diversity (Buisson et al. 2021). Therefore, preventing land conversion should be prioritized (Carbutt & Kirkman 2022, Slooten et al. 2023). Tropical grasslands are increasingly being targeted for afforestation and carbon-offset projects, fueled by

the misconception that these ecosystems are degraded forests (Veldman et al. 2015, Bond et al. 2019). Ecologically misinformed afforestation leads to loss of biodiversity and ESs (Veldman et al. 2015) and can contribute to catastrophic megafires (Stevens & Bond 2024). Instead, restoration and carbon-capture projects in tropical grasslands should aim at restoring the diversity of forbs and other important species in the herbaceous layer (Nerlekar et al. 2024b) in light of detailed knowledge about their contributions to ecosystem integrity and ES delivery.

5. CONCLUSION

Forb ecology is a young research area in tropical grassland ecosystems but a growing focus that is increasingly clarifying the functional importance of herbaceous plants beyond grasses. In this review, we highlight key functional roles of forbs. Overall, the available evidence suggests that forbs in tropical grasslands play a major role in maintaining biodiversity and ecosystem functioning and in supporting and enriching human lives, as they have for millennia. The available evidence indicates that forbs in tropical grasslands collectively have traits that help them to continue their offerings to future ecosystems and human generations; however, a complete accounting and understanding of their contributions to ecological processes requires more work. With this in mind, we list several topics as future issues that we consider knowledge gaps in need of attention to improve our ecological understanding of tropical grasslands and safeguard the delivery of ESs in grasslands globally.

FUTURE ISSUES

1. To underpin the functional importance of tropical grassland forbs, keystone species (e.g., Narango et al. 2020) and/or keystone functional groups (e.g., Lavorel et al. 2015) need to be identified across spatial scales, for instance, by identifying forb species and/or functional groups with multiple roles and functions, e.g., medicine, food, carbon storage, animal fodder, etc.
2. Knowledge of regeneration and reproduction strategies of forb species in tropical grasslands is required to improve our understanding of their long-term persistence. In particular, documenting belowground traits, such as bud banks, organ types and clonality, will inform exploration of (*a*) aboveground regrowth rates and biomass production after damage and (*b*) whether clonal multiplication comes at the expense of seed production.
3. Understanding of seed ecology and seed-bank dynamics in tropical grassland forbs is limited. More extensive seed studies, including mechanisms of seed dormancy, are essential to establish seed-bank repositories for restoration.
4. The functional role of forbs in climate change mitigation needs further exploration. The contribution of long-lived perennial forbs to carbon cycling and carbon storage may be substantial but remains poorly documented. Although several sources claim that USOs contribute substantially to the belowground carbon pool, this contribution remains to be accurately quantified across regions. Furthermore, there is a limited understanding of the resorption of nutrients, age, and decomposability of USOs. Community-level assessments are required to model projected carbon inputs of forb communities under changing climate scenarios.
5. Herbivore–forb interactions have received growing attention over the past decade. Herbivores, from livestock and other large mammals to rodents and insects, use forbs as

forage and medicine, but the nutritional contribution and, especially, the mechanisms of self-medication are not well understood. The ways in which insect herbivory has shaped pollination syndromes in forbs are better documented than the ways in which large herbivores have shaped the reproductive strategies and functional diversity of aboveground plant parts.

6. The interactions between belowground herbivory and the ecology and evolution of forbs have received limited attention in tropical grasslands. Persistent, intense belowground herbivory is expected to affect the woodiness of storage organs, the content of secondary metabolites, the depth of the organ placement, and the relationship between size and number of USOs.
7. Human dependence on tropical grassland forbs as food and medicine may be underestimated, especially in semiarid and arid regions. Acknowledging and respecting indigenous knowledge are essential to contribute to a more comprehensive account of useful tropical grassland forbs, their sustainable use, and conservation.
8. Biogeographic unevenness in research effort across tropical grasslands, especially outside of southern Africa and South America, impedes a unified understanding of forb ecology. More studies on the role of forbs in ES delivery and functioning are needed from the southern extent of tropical grasslands in North America, northern and western Africa, Asia, and Australia.

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