PERSPECTIVE

The history and challenge of grassy biomes

Grassy biomes are >20 million years old but are undervalued and under threat today

By **Caroline A. E. Strömberg**[1]
and **A. Carla Staver**[2,3]

Grassy biomes—from the steppes of Mongolia to the savannas of Tanzania—are predicted to be the ecosystems hardest hit by the ongoing climate and land use crises. The history of humans has been profoundly intertwined with grassy biomes. *Homo* evolved in the savannas 2 million years ago (Ma), and agricultural societies arose through the domestication of grasses, such as wheat and barley, 10,000 years ago. These grass crops, as well as corn and rice, remain dominant staple foods globally (*1*). Livestock production also centers in areas that were once (and sometimes still are) native grasslands. Grassy biomes harbor distinct and diverse sets of plants and animals that have adapted to these environments through millions of years of evolution (*2*). As the biodiversity and economic prominence of grassy biomes are increasingly being recognized, there is a demand for better understanding of their past and present function to inform policy and management.

Grassy biomes are biogeographically widespread, accounting for >25% of all land on Earth, including 35% of the tropics and subtropics. The emergence of grassy systems during the Cenozoic (the past 66 million years) was complex, shaped by climate, soils, fire, and herbivory in ways that are not fully understood (see the figure). Clarifying these mechanisms will be key for managing the fate of grassy biomes under ongoing and future environmental changes that are driven by human activities.

Grasses, defined as plant species in the family Poaceae, originated by the Late Cretaceous (100 Ma) (*3*) but did not become ecologically dominant until >70 million years later, in the later Cenozoic. This exceptionally long lag has prompted evolutionary biologists and paleontologists to search for the drivers that allowed grass to reach its current global prominence. Today, most grasses are associated with open-canopy habitats, owing to several traits acquired relatively early in Poaceae evolution (100 to 60 Ma) (*1*, *3*). For example, grasses may have quickly evolved a rapid life cycle and persistent buds, permitting quick regrowth after drought, frost, or disturbances such as fire and grazing. Starting by 55 Ma, several groups of grasses evolved so-called C_4 photosynthesis (as opposed to C_3 photosynthesis), which allows them to prosper in hot and dry areas (*1*). In colder climates, C_3 open-habitat grasses developed the tolerance needed to survive frosts by 30 Ma (*4*). However, although the evolutionary traits suited to open habitats appeared earlier, open-habitat grasses remained ecologically rare until later in the Cenozoic.

Once grasses started spreading across the globe, their takeover was asynchronous and followed continent-specific trajectories. For instance, grassy habitats appeared in North America by 25 Ma but not until 7 Ma in Australia (*5*, *6*). However, the first subtropical grassy biomes were unlike anything observable there today, featuring C_3 open-habitat grasses that today are found in colder regions (*6*). It was not until several million years later that tropical open-habitat C_4 grasses expanded to form grasslands and savannas at low to mid-latitudes (*5*, *7*), roughly coincident with the spread of frost-tolerant grasses at higher latitudes.

Grassy biomes thus emerged during the Cenozoic at different times in different places and, at least in part, for different reasons. Studies in modern grassy biomes suggest that aridity and rainfall seasonality, as well as fire and herbivory, could all favor grasses over trees (*2*), with even larger benefits at lower atmospheric CO_2 concentrations. The fossil record shows that many of these conditions did occur in the late Cenozoic. By 34 Ma, atmospheric CO_2 levels had dropped, and the globe underwent a period of cooling. In many areas, altered atmospheric circulation and mountain uplift (e.g., of the Tibetan Plateau) resulted in aridification or seasonal drought, and fossil evidence indicates increased fire activity near the end of the Cenozoic (*5*). Further, large grassland-type mammal herbivores (e.g., bovids) diversified during the mid- to late Cenozoic (*8*).

Asynchrony in the emergence of grasses on different continents suggests that, although global factors such as low-CO_2 conditions may have spurred the diversification and expansion of open-habitat and especially C_4 grasses (*7*), changes in CO_2 were typically not enough to allow grasses to dominate. A rapidly expanding geochemical and paleontological tool kit has allowed for more detailed insights. Studies have shown that regional changes in climate and fire interacted with existing vegetation to influence trajectories of emerging grass dominance, with divergence across continents. For example, the earliest North American C_3 grassy habitats replaced forests as seasonal drought developed (*6*), and in Australia, C_4 grasses favored by pronounced aridification overtook fire-adapted eucalypt woodlands that had existed there for tens of millions of years before (*5*). By contrast, in South Asia and southwest Africa, more frequent and intense wildfires promoted replacement of fire-sensitive vegetation with grasses (*9*), suggesting a substantial regional, if not global, role for fire.

In addition to environmental conditions, herbivores may also have directly contributed to the spread of grassy vegetation, although the mechanisms are not yet understood. Defense strategies against herbivores by savanna trees, such as growing spines or thorns, evolved concurrently with the spread of grasses and the diversification of bovids in Africa (~17 Ma) but long before fire activity increased (*8*). This suggests that, at least in Africa, herbivores structured grassy biomes before fire did. However, just how important animals were in shaping the evolution of grassy vegetation remains untested and will require adapting methods of estimating past herbivore intensity (such as studying fungal spores in fossilized dung) for Miocene and older samples.

Since they first appeared, grassy biomes have continued to shift in extent, structure, and composition, prompted by advancing and retreating ice sheets during the global Ice Age (2.6 Ma onward). Today, they are widely distributed on every continent except Antarctica, with a range in part associated with aridity and rainfall seasonality. Some 60% of grassy ecosystems receive <750 mm of annual rainfall, most with a dry season that shapes plant physiology. This provides a rationale for the argument that aridity drove late Cenozoic grassland expansion. However, 40% of grassy ecosystems extend into higher-rainfall regions with >750 mm of annual rainfall that can support forests. These moderately wet, or "mesic" grassy ecosystems are biogeographically distinct from semiarid ones, but both are evolutionarily ancient (*1*). Yet, whereas

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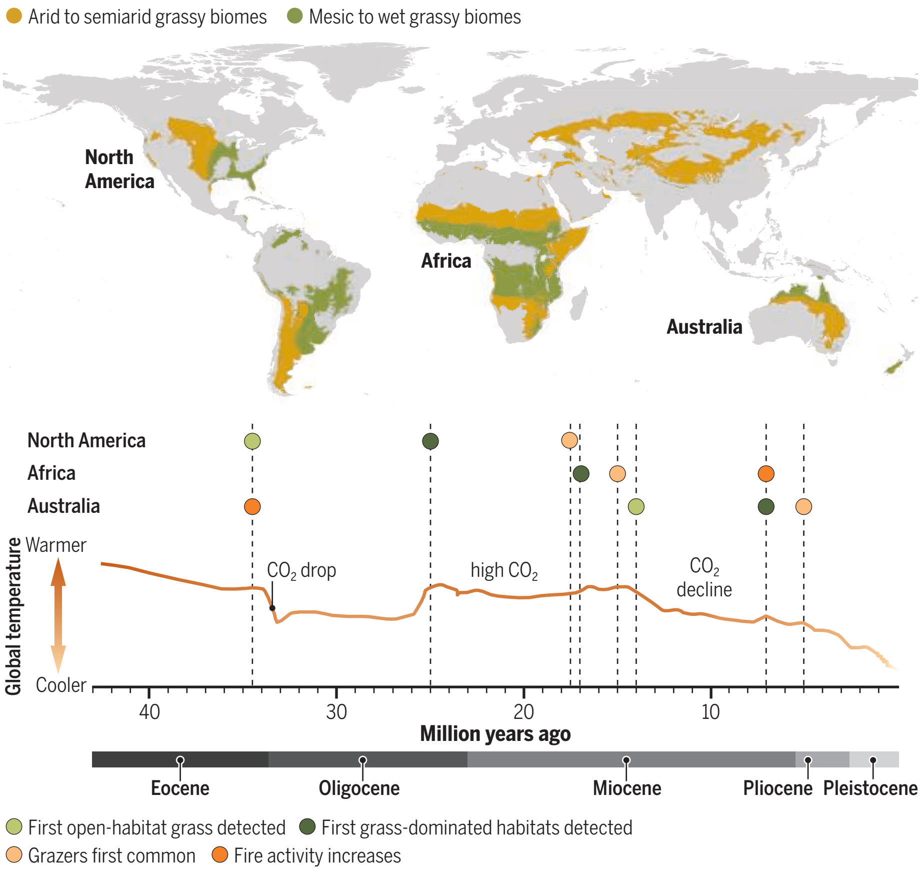
[1]Department of Biology, Burke Museum of Natural History and Culture, University of Washington, Seattle, WA, USA. [2]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA. [3]Yale Institute for Biospheric Studies, Yale University, New Haven, CT, USA. Email: caestrom@uw.edu; carla.staver@yale.edu



The history and legacy of grassy biomes

Grassy biomes exist in a wide range of climates, from cold to hot and arid to wet (top). Although changing environmental conditions through time have shaped their past and present distribution, disturbance regimes (fire, herbivory) and vegetation histories also shaped their evolution and current and future function (bottom).

GRAPHIC: K. FRANKLIN/SCIENCE; (DATA) KARP ET AL. (5); KUKLA ET AL. (6); CHARLES-DOMINIQUE ET AL. (8); HOETZEL ET AL. (9)

semiarid savannas are widely accepted as the native vegetation of large areas of the globe, mesic savannas were long assumed to represent degraded forests. Only recently have mesic savannas been acknowledged for their contributions to endemic biodiversity and distinctive ecosystem function.

As their antiquity is increasingly recognized, the ecological processes that promote mesic savanna stability have come into increasing focus (*2*). Fire likely plays an important role in stabilizing mesic savannas, excluding forests by preventing tree establishment or killing trees, thereby favoring grasses. In total, grassy biomes make up >80% of the global burned area annually. Experiments, field observations, and remote sensing analyses all support fire as a mechanism allowing grassy ecosystems to expand into mesic regions. Plant traits are consistent with the history of fire in mesic savannas. The distinct, diverse, and ancient tree and shrub communities (*8*) are well adapted to enduring fires with thick bark, large belowground nonstructural carbohydrate reserves, and bud banks that promote resprouting. In addition to tolerating fire, many grasses actively spread fire (*10*). These fire adaptations have major implications for the ecosystem functioning of grassy biomes. For instance, the large belowground reserves in grassy biomes may mean a substantially larger belowground carbon storage compared with that in other biomes (*11*). Current estimates suggest that grassy biomes hold at least 17% of global biomass carbon (*12*), but this is certainly an underestimate (*11*) that needs to be adequately quantified so that the potential role of grassy biomes as carbon sinks can be fully appreciated.

Herbivores that graze on grass and eat tree leaves also influence grassland function (*13*), especially in semiarid savannas, where grass eaters decrease grass biomass accumulation and tree eaters prevent trees from establishing. Abundant herbivory-related traits have accumulated over evolutionary time in grassland plants, including herbivory defenses in trees (e.g., spines) (*8*) and grass morphologies that withstand intense grazing (e.g., growing from the base instead of from shoot tips and bud banks for resprouting) (*1*). Nevertheless, the importance for grassy biome distributions of herbivory relative to other factors, such as climate and soil conditions, remains an open question.

Overall, evidence is converging around the idea that grassy ecosystems are complex, with ecologies that depend not just on climate but also on interactions and feedbacks with fire and herbivory. These ecologies are profoundly influenced by the evolutionary history and resulting trait diversity of regional biota (*1*). Their complexity makes predicting the responses of grassy biomes to global change a particular challenge. Nonetheless, studies have shown that the combination of CO_2 fertilization, fire suppression, and livestock extensification has resulted in widespread woody encroachment (*14*) and associated degradation of grassy biomes—a trend that will likely continue into the near future.

Grassy biomes are also threatened by ongoing land use conversions and degradation while being among the least protected globally (*2*). For example, 90% of temperate grasslands have been transformed into agricultural or urban areas, with <1% of remnants currently protected from land development. Whereas rainforests in the Amazon have attracted widespread attention from the popular media, the ongoing threat to savannas, especially in Africa, South America, and Asia from afforestation, fire exclusion, and land use conversion, has gone unnoticed. The effects on savanna and grassland biodiversity will be devastating; for instance, 40% of grassland vertebrate species are projected to be lost by 2070 (*15*). Thus, the fate of evolutionarily ancient grassy biomes hangs in the balance, with terminal consequences for their functionally and evolutionarily distinct biota. ■

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