The paradox of forbs in grasslands and the legacy of the mammoth steppe

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The grassland biome supports an enormous diversity of life and includes ecosystems used extensively by humans. Although graminoids lend grasslands their characteristic appearance, forbs are largely responsible for their taxonomic, phylogenetic, and functional diversity. In terms of abundance, however, forbs often play a subordinate role relative to graminoids. Yet this may be a relatively recent phenomenon; evidence is mounting that forbs comprised a major part of the richness of, and were abundant in, the extensive and highly productive grasslands of the Pleistocene, the so-called "mammoth steppe". As a legacy of their past prevalence under intensive grazing by megafaunal herbivores, we hypothesize that forbs were, and still are, dependent on niche construction by large mammalian herbivores. We suggest that the high species richness of forbs in grasslands globally merits greater research and conservation attention, and management actions tailored to sustain their abundance and diversity.

Grasslands represent one of the most important biomes on Earth, both in terms of areal extent and the ecosystem services they provide (sensu Bond and Parr 2010). Pressures on the grassland biome, including land use, climate change, invasive species, and nitrogen (N) deposition, are widespread and have contributed to major declines in grassland biodiversity globally (Gibson 2009; Duprè *et al*. 2010; Gibson and Newman 2019). This decline is particularly strong among forb species (defined as non-graminoid, herbaceous, angiosperm species; Bond and Parr 2010). Even the abandonment of agriculture represents a source of pressure on grasslands, leading to such extensive impacts on biodiversity that several forb species are now on the edge of extinction (Eriksson 2013). To better understand how human-related pressures are affecting grassland biodiversity, and how these pressures can be mitigated, scientists and resource managers will require new insights into how grasslands function.

Conditions for grassland plant communities that are prevalent today, in the Anthropocene, have no analogous period in the past for comparison. Yet selection pressures under which grassland species typically evolved, and to which they are likely still adapted, can inform management options. Therefore, inspired by the advocacy to merge paleobiology with conservation biology (Barnosky *et al*. 2017), we make an interpretation of grassland functioning based on the legacy of the "mammoth steppe". The mammoth steppe of the Pleistocene is an ecosystem regarded as paramount because it sustained much of the now-extinct megafauna of that epoch. The traditional view of graminoid dominance (eg Zimov *et al*. 1995; Blinnikov *et al*. 2011) on the mammoth steppe is currently being reevaluated in light of new DNA-based research that suggests that the mammoth steppe was in fact dominated by forbs, in terms of abundance, species diversity, and proportions of the megafauna diet (Willerslev *et al*. 2014). Moreover, although the mammoth steppe has no contemporary analog, many of the forb and graminoid species identified from Pleistocene grasslands are still part of contemporary flora (Willerslev *et al*. 2014). Here, we apply recent advances in our understanding of the mammoth steppe to illustrate the potential role of forbs in contemporary grassland functioning. We also consider the extent to which past selection pressures on forbs, which they evidently tolerated, are absent in contemporary grasslands. In doing so, we argue that forbs should receive greater attention in grassland research and management if the biodiversity and functioning of the grassland biome is to be conserved and sustained in the future (Siebert and Dreber 2019).

Consistent with previous studies of grassland systems, we consider forbs as a single functional group. Yet our primary objective is to inspire greater interest in the *diversity* of forb

In a nutshell:

- Forbs contribute substantially to the taxonomic, phylogenetic, and functional diversity of contemporary grasslands, yet as a guild they are largely inferior in abundance
- Contemporary forbs flourished in the highly productive "mammoth steppe" grasslands of the Pleistocene epoch, suggesting they are adapted to niche construction by herbivorous megafauna
- As a legacy of their past prevalence during the Pleistocene, forbs in contemporary grasslands likely still depend on the presence of selection forces resembling megafaunal activities
- Greater research and management attention should be directed toward forbs to conserve the biodiversity and functioning of the grassland biome

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species and their role in grasslands to improve understanding of plant diversity and function in these imperiled ecosystems.

◼ The "paradox" of forbs

The high abundance of grasses in contemporary grasslands is explained by functional traits that help them colonize, persist in, and transform grasslands (Linder *et al.* 2018). However, traits that provide grasses with a competitive advantage, such as photosynthesis via the C_4 carbon fixation pathway, are more common among forb than grass lineages (Sage 2004). As discussed below, forbs have several functional traits that are seemingly contradictory to their subordinate ranking in terms of abundance: we call this the "paradox" of forbs (Figure 1).

Contribution of forbs to grassland diversity

In terms of species richness, forbs dominate grasslands worldwide and across a wide range of climate regimes (Figure 1a; Seabloom *et al.* 2013). Forbs are the most species-rich growth form in many grasslands, including North American prairies; African savannas; South African velds; tundra grasslands; Iberian dehesas; Mongolian steppes; South American pampas, campos, and cerrados; and calcareous grasslands, grassy balds, and other environments (WebTable 1a). Forb species richness may even be underestimated, as many forb species in grasslands are ephemeral (Pokorny *et al.* 2004), having shallow roots and short life cycles that render them transient or unobservable for much of the year.

Forbs also contribute greatly to the phylogenetic richness of grasslands. Although graminoids are often presented taxonomically by family names, this approach is impractical for forbs because of the vast number of families (Panel 1). The term "forbs" oversimplifies their diversity in grasslands, where their high phylogenetic richness suggests they likely serve a wide range of functional roles. In an analysis of ecophysiological and ecological traits of 158 prairie species, most segregated functional groups were forbs (Figure 1b; Kindscher and Wells
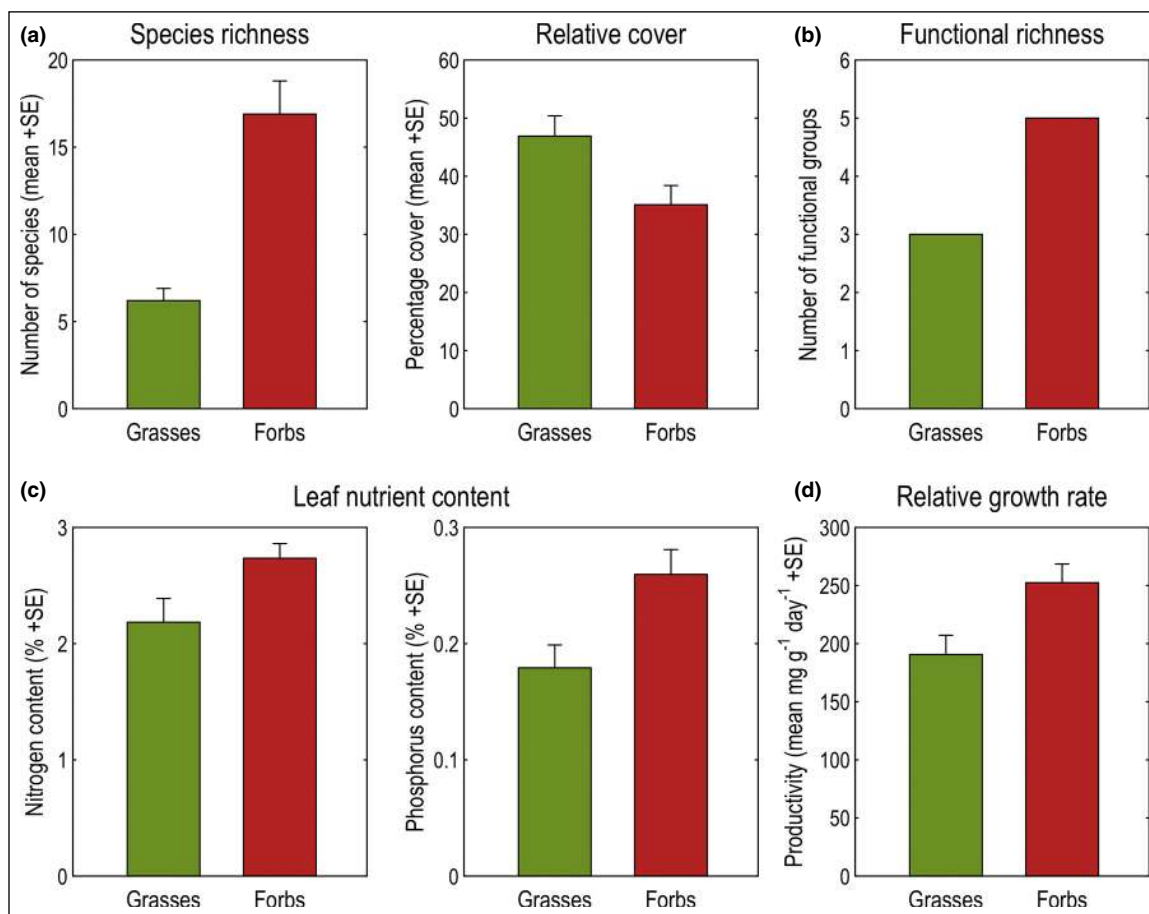

Figure 1. (a) Average species richness (number of species per square meter) and cover (%) of forbs and grasses across 62 contemporary grasslands spanning six continents and 13 countries (data from Seabloom *et al.* [2013], which relied on sites within the Nutrient Network [http://nutnet.org], a globally replicated study of grassland ecosystems). (b) Number of plant guilds, or functional richness, based on a multivariate analysis of 32 traits from 158 native prairie species (data from Kindscher and Wells [1995]). (c) Leaf nutrient content in forb (*n* = 52) and grass (*n* = 14) species in alpine tundra grasslands; samples were from early and late growing seasons combined (data from Murguzur *et al.* [2019]). (d) Relative growth rates of forb (*n* = 13) and grass (*n* = 11) species reported from an experiment where plants were provided with ample resources from the seedling stage (data from Poorter and Remkes [1990]). Similar results as in (c) and (d) but at a global scale were reported by Niinemets *et al.* (2015). Where present, error bars indicate standard error (SE).

Panel 1. What defines forbs and graminoids in grasslands

We define "grasslands" as encompassing steppe, prairie, veld, pampas, savanna, cerrado, balds, dehesas, poloninas, and nonacidic tundra ecosystems. Grassland systems are present on every continent except Antarctica (Gibson 2009).

Graminoids dominate grasslands, especially grasses (species of Poaceae in the Order Poales), but sedges (Cyperaceae) and rushes (Juncaceae) – both members of the Poales as well – also occur frequently (Gibson 2009). Grasslands are conceptually linked to large mammalian grazers. Emphasizing our long understanding of grasses as important to grazing, the word "grazer" is derived from the Old English word "græs", meaning "grass".

Forbs comprise a huge variety of species and plant families in grassland ecosystems. Apart from the Fabaceae (legumes), a family more species-rich than the Poaceae (www.mobot.org/MOBOT/research/APweb), forbs are seldom referred to by family names but rather by general terms like forbs, herbaceous (as opposed to woody) forbs, non-graminoid herbaceous species, herbaceous dicotyledons, and non-graminoid monocots, as well as by more imprecise terms like herbs (includes all herbaceous species) and dicots (includes woody species). Despite their enormous variety, forb species are often lumped into a single category; moreover, forbs are often listed as "other" constituents of grassland plant communities (Pokorny *et al.* 2004; Siebert and Scogings 2015) or even as weeds (Gibson 2009).

1995). In addition, studies showing positive effects of plant biodiversity on ecosystem services, implying multifunctionality, typically involve grassland experiments in which forbs represent ≥50% of the species pool (eg Reich *et al.* 2012; Weisser *et al.* 2017).

Role of forbs in grassland plant–herbivore interactions

As a species-rich guild with a long co-evolutionary history with herbivores (Veldman *et al.* 2015), forbs have evolved a diverse array of adaptations to herbivory. For instance, physical and chemical defenses are common among forbs (eg Strauss *et al.* 2002), and several unpalatable forb species have gained dominance in grasslands, to the detriment of grassland quality for ungulate herbivores (Augustine and McNaughton 1998). However, although anti-herbivore defenses are considered to be a critical distinction between grasses and forbs (eg Coughenour 1985), grasses have also evolved numerous physical and chemical defenses (Vicari and Bazely 1993; Massey *et al.* 2007).

Forbs can also be both highly palatable and tolerant to grazing, the latter a very important trait in grassland plants (Augustine and McNaughton 1998). In terms of compensatory growth, tolerance is often linked to graminoid basal leaf meristems, which make graminoids well adapted to regrow after defoliation (Hawkes and Sullivan 2001). A stricter definition of tolerance is the degree to which plant fitness is affected by herbivore damage relative to fitness of undamaged plants (Strauss and Agrawal 1999); under this definition, tolerant species more often include forbs (Hawkes and Sullivan 2001). Several forb species have even been found to increase their fitness when grazed (WebTable 1b), typically through damage to apical meristems, which activates dormant buds (Wise and Abrahamson 2008). Consequently, tolerance (in terms of growth rate) to herbivory can be high among grasses, whereas tolerance (in terms of fitness) to herbivory in grasslands can be high among forbs. Furthermore, forbs have on average the highest tissue N and phosphorus (P) concentrations, and the fastest growth rates among plant growth forms

globally (Figure 1, c and d; Niinemets *et al.* 2015). As such, forbs are very nutritious, and rank high in herbivore diet selectivity among plant growth forms (WebTable 1c). Grassland forage quality, in terms of optimal nutrient balance for herbivores, is therefore improved by the inclusion of nutritional forbs in forage. Finally, forbs seem to benefit from many herbivore behaviors that disturb the soil (eg trampling, wallowing, uprooting, digging; also known as niche construction or ecosystem engineering). These actions promote grassland plant richness (Romero *et al.* 2015), and forbs in particular are proficient at exploiting these herbivore-created opportunities for establishment. For example, forbs are the most species-rich and abundant growth forms in patches of disturbed soil like prairie dog (*Cynomys* spp) colonies (Coppock *et al.* 1983) and bison (*Bison* spp) wallows (McMillan *et al.* 2011). Megaherbivores like elephant (*Loxodonta* spp), giraffe (*Giraffa* spp), and black rhinoceros (*Diceros bicornis*) rework soils in African savannas, increasing forb species richness and abundance (WebTable 1d). In turn, herbivores seem to spend more time on patches of disturbed soil than on surrounding grassland (Fahnestock and Detling 2002; Porensky and Veblen 2015), suggesting that herbivore-created patches rich in forb species diversity and abundance represent nutritional hot spots for herbivores.

Adaptation among forbs to fire and herbivory

Grassland plant species also have a long evolutionary history with fire (Veldman *et al.* 2015). Several forb species have underground storage organs that increase their resilience to fire (as well as to herbivory and drought; Bond and Parr 2010), and several forb species are adapted to cues from fire for sprouting and seedling recruitment (Bond and Keeley 2005). Perhaps for this reason forbs can tolerate a wider range of seasonal conditions and fire frequencies than dominant grasses, and therefore benefit from fire events (Uys *et al.* 2004). Forbs can also better tolerate the dual impacts of fire and herbivory; although recently burned areas are favored grazing spots for

herbivores, they are also characterized by increases in both forb richness and abundance (Fuhlendorf and Engle 2004).

A critical role of forbs in grasslands

The aforementioned facts are based on studies that draw attention to the critical role that forbs play in grasslands. However, given their high species, phylogenetic, and functional richness, why forbs are not more abundant in grassland systems remains a mystery. That is, the superior richness of forbs could be expected to guarantee good performance under a set of ecological contexts and species interactions, causing their abundance to be more aligned with their richness. Looking at the past conditions and selection pressures under which forbs thrived could provide some clues toward solving this puzzle.

Interpretation of paleoecological evidence

The mammoth steppe covered a vast geographic area and sustained megafauna in a climate that was colder and drier than the present Arctic; how this was possible has been referred to as the "productivity paradox" (Yurtsev 2001). The megafauna community itself likely played a central role in maintaining the high productivity of the mammoth steppe. According to the "keystone herbivore hypothesis" (analogous to the effects of large African ungulates and other herbivores; Owen-Smith 1987), the megafauna generated disturbances and modified the environment through numerous behaviors and activities. Their grazing and trampling would have facilitated sunlight reaching ground level by preventing competitive plants from growing tall, while trampling would have pushed litter into the soil and generated gaps for new plant recruitment. Urination and defecation returned nutrients in a form readily available for plant uptake, increasing rates of nutrient cycling (Bardgett and Wardle 2003). Finally, megafauna would have facilitated seed dispersal (Yurtsev 2001), providing opportunities for plant species to establish in new sites. We hypothesize that such niche construction/ecosystem engineering by the megafaunal community would have exerted strong selection pressures on grassland plants (Figure 2). That forbs were dominant on the mammoth steppe, in terms of abundance, diversity, and megafauna diet composition, suggests that they were both thriving under these selection pressures and central to the high productivity of the steppes (Willerslev *et al.* 2014). In addition to direct herbivory, by altering the quantity and distribution of fuel supplies, large herbivores could shape the frequency, intensity, and spatial distribution of fires on the mammoth steppe (Waldram *et al.* 2008). Because fire and herbivory share several common features, fire could have further enforced key selection pressures (Augustine and McNaughton 1998; Weigl and Knowles 2014); for instance, like herbivory, fire events enhance light availability at ground level, thereby creating more opportunities for plants to germinate, bud burst, and grow.

Other ecosystem characteristics, especially those related to high species richness, may also have been key to the high productivity of the mammoth steppe. A wealth of evidence shows that high plant species richness increases grassland functioning through complementarity effects, and promotes temporal stability of aboveground net primary productivity, efficient nutrient recycling by decomposer communities, and increased soil carbon storage, among other processes (eg Weisser *et al.* 2017). The richness and abundance of forbs on the mammoth steppe would likely have sustained higher species diversity as a result of collective feedbacks within their communities (Bråthen and Ravolainen 2015). Furthermore, the actions of mammalian herbivores (eg grazing, trampling) would have helped to sustain plant diversity. Selective grazing is less likely when plant species richness is high, even among species that produce high concentrations of secondary metabolites (Wang *et al.* 2011), and both palatable and unpalatable species are affected by trampling (Owen-Smith 1987). Strong plant–herbivore interactions promoting forb and graminoid species richness and ecosystem functioning may therefore have been key to the high productivity of the mammoth steppe (Figure 2).

In our interpretation, the mammoth steppe can be viewed as a grassland of low standing biomass with ample light conditions at ground level; it would be highly productive, but not visibly so because a large fraction of what was produced was consumed or trampled into the ground (Figure 2, bottom panel); and conditions promoting safe sites for plant recovery and regeneration would produce a visible range of growth stages and high species richness. Well-functioning plant–herbivore interactions that imply a high plant species turnover, both spatially and temporally, were integral to the mammoth steppe (Figure 2). This complex and highly dynamic system would foster conditions under which a range of forb and graminoid species coexisted.

Limiting factors for forbs in contemporary grasslands

We suggest that forbs of contemporary grasslands may be anachronistic species that have been in decline since the time of the Pleistocene megafaunal extinctions (Johnson 2009). Because of the global occurrence of both high forb species richness in grasslands (Figure 1a) and the extinction of megafauna (Sandom *et al.* 2014), we posit that various guilds of forbs are still adapted to and largely dependent on the niche construction provided by megafauna. In the following sections, we identify conditions that were likely present in the Pleistocene but are potentially absent in contemporary grasslands, and in doing so, suggest possible reasons for the current subordinate-level abundance of forbs.
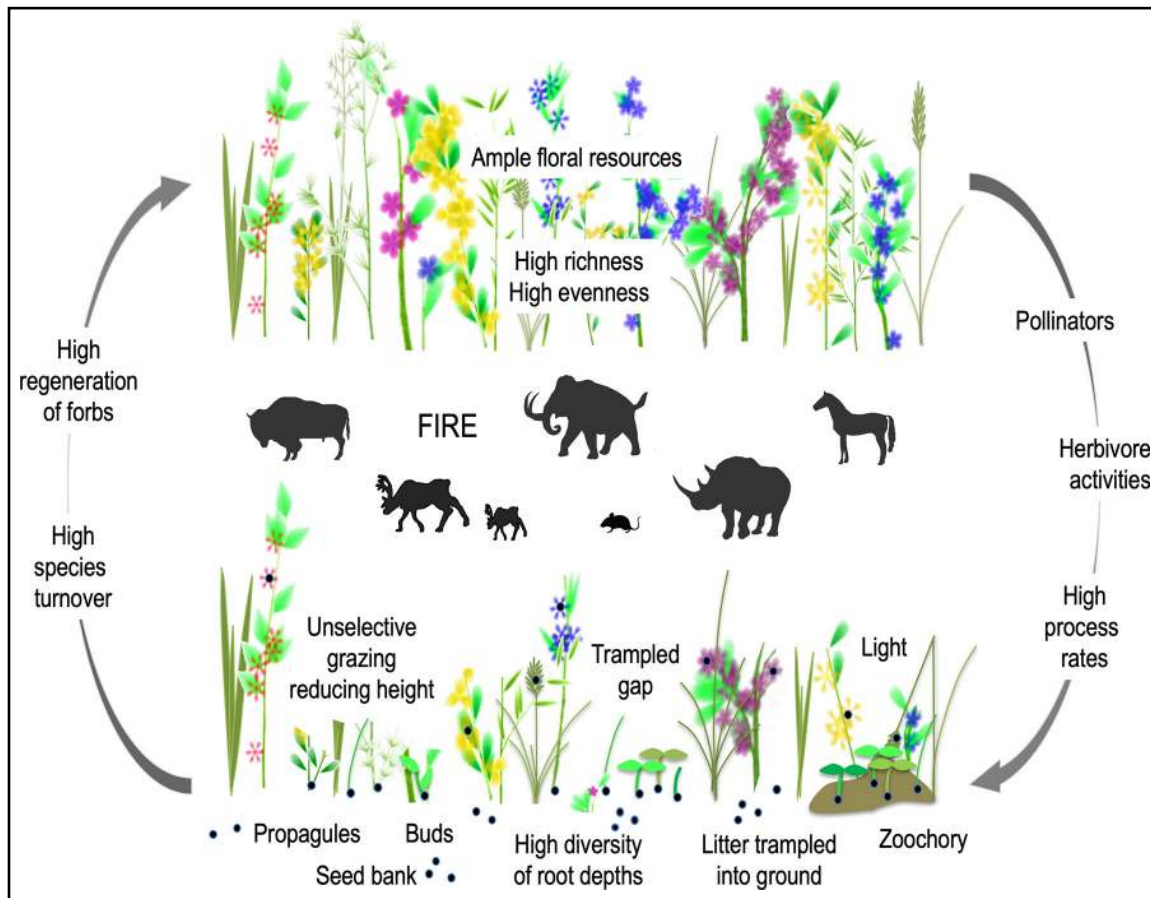
Figure 2. Strong plant–megafauna feedbacks in the mammoth steppe. A species-rich, forb-rich plant community with high process rates represents nutrient-rich and diverse forage for megafauna; in turn, megafauna disturb the plant community through a range of activities. Grazing and trampling increase accessibility to light: trampled gaps and litter trodden into the soil create sites for seed germination and bud bursting (solid black circles). Urination and defecation fertilize vegetation and seeds are dispersed by endozoochory (black circles in brown mound) and epizoochory. Megafauna activities may have been responsible for a substantial portion of the niche construction that occurred on the mammoth steppe.

Herbivore size and diversity

In the Pleistocene, megafauna had a median body weight of ~182 kg, but by the late Holocene the median body weight of grassland mammals had fallen to 0.7 kg, and is even lower in contemporary grassland systems (Dirzo *et al*. 2014). Trampling by megafauna and other fauna therefore had potential to create soil disturbance beyond that possible in most contemporary grasslands, where herbivores are much smaller and lighter. Along with declines in herbivore size, herbivore species and trait diversity have also declined (Dirzo *et al*. 2014). Such reduced herbivore activity has been an integral part of contemporary grassland development, during which time the shift in forbs from dominance (cf Willerslev *et al*. 2014) to a subordinate position (cf Seabloom *et al*. 2013) in terms of abundance has also occurred.

While less intense and less diversified levels of mammalian herbivory may have reduced niche construction capacity relative to that of earlier herbivore guilds, humans have also played an increasingly important role in shaping grassland systems. According to Eriksson (2013), land use by humans in the pre-agricultural landscape of northwestern Europe favored open pastures and fields that harbored a diversity of plant species. At the onset of the Holocene, human-mediated niche construction gradually became more important; in addition to grazing management, humans were using fire and cutting vegetation manually to facilitate spatially stable and interconnected grasslands (Gibson 2009; Eriksson 2013). The continuous existence of grasslands from the Pleistocene to the Anthropocene in which forb and graminoid growth forms are common suggests similar niche construction forces have been, and continue to be, present across grassland types despite different histories.

In northwestern Europe, the cessation or alteration of human land use in recent decades has reduced niche construction, with a concomitant loss of subordinate species (Eriksson 2013; Weigl and Knowles 2014). For instance, the forb *Gentianella campestris* is highly tolerant to grazing, but continuous grazing throughout the growing season, as opposed to seasonal grazing and cutting, has caused this species to decline to such an extent that it is now listed as an

at-risk species (Lennartsson and Oostermeijer 2001). Continuous grazing reduces the time for plants to recover and reproduce (Gibson 2009), and recovery time can be especially short for rare, high-quality plant species – such as forbs – that are selectively grazed (Figure 3; Olff and Ritchie 1998). Less diversified levels of herbivory and fire, along with reductions in cutting practices, have likely caused more uniform pressures on grasslands; palatable forbs may also be less tolerant of such conditions.

Conditions for plant survival, growth, and reproduction

To persist in a community, plants generally need time and resources to recover after grazing or cutting, from seeds, buds, or regrowth, but specific requirements differ markedly between species and contexts (Strauss and Agrawal 1999; Wise and Abrahamson 2008). The effect of herbivores on forb abundance in contemporary grasslands is therefore likely to be highly context dependent (Hawkes and Sullivan 2001), and in particular contingent on the functional traits of dominant plant species (Avolio *et al*. 2019). In grasslands globally, large mammalian herbivores (adult body mass >45 kg) and herbivore richness reduce dominant plant species to the extent that plant species richness is promoted (Koerner *et al*.

2018), suggesting competitive effects of dominant plants are important in limiting resource availability to both grazed and ungrazed forbs.

Lack of regeneration possibilities is an important factor contributing to the low abundance of forb species in contemporary grasslands. Seedling establishment of subordinate or transient forbs, as with other species, is often constrained by the availability of safe germination sites or gaps (Figure 3; Olff and Ritchie 1998; Turnbull *et al*. 2000), but gaps are not simply open spaces, as roots or other plant organs may be present below the ground surface, preventing seedling establishment (Armas and Pugnaire 2011). Clonal rhizomatous plants, including several dominant grasses, often occupy upper soil horizons, giving them a competitive advantage and the capacity to suppress plant species richness (Figure 3; Eilts *et al*. 2011). Disturbances that disrupt belowground plant dominance, such as the activity of herbivores, can generate sites safe for forb germination. As Grime (1998) stated, "the persistence of subordinates in…grassland…vegetation is frequently dependent upon periodic events (disturbance) that temporarily restrict the vigor and competitive effects of dominant plants". Such disturbance of vegetation can also facilitate regeneration from buds (Klimešová and Klimeš 2007; Wise and
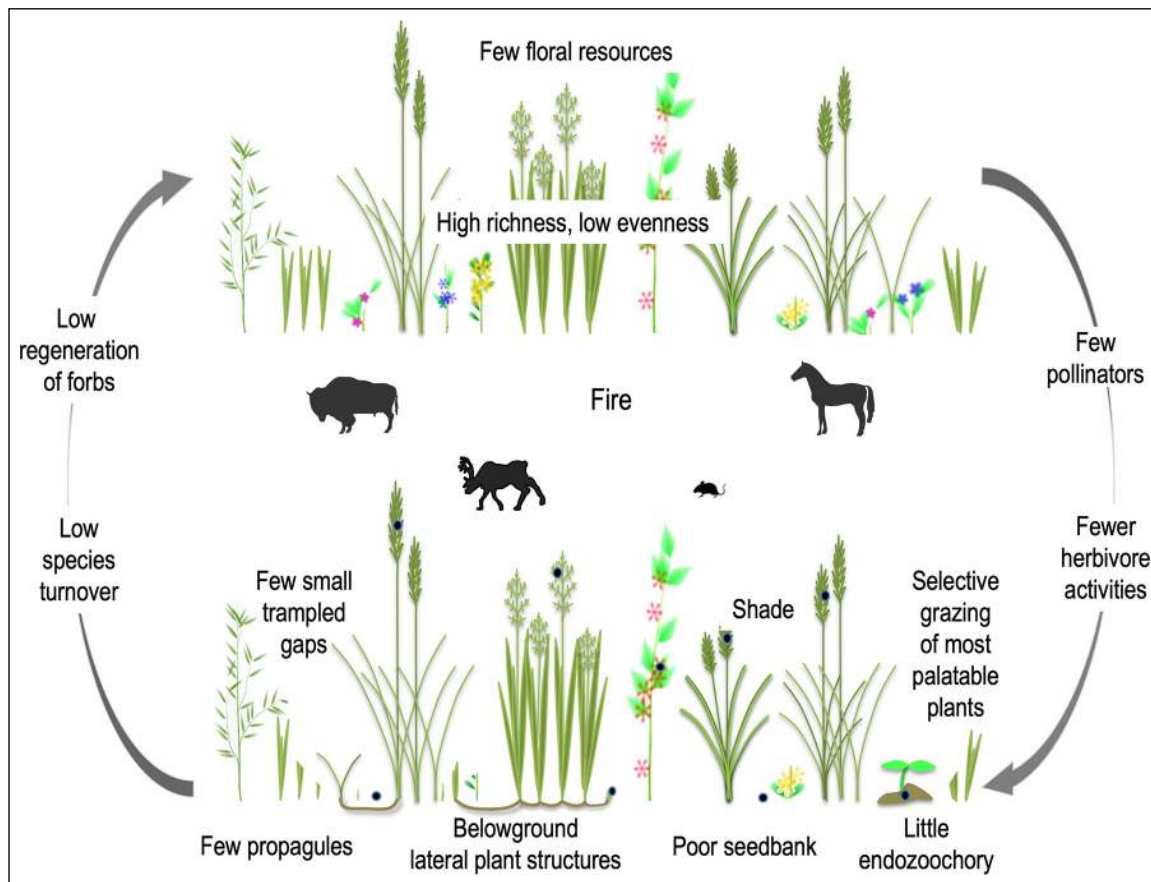
Figure 3. Weak plant–herbivore feedbacks in contemporary grasslands. Forb populations are assumed to be small and fragmentary, as they are part of the subordinate or transient species pool under strong competition from dominant species of caespitose and rhizomatous graminoids (or the occasional dominant forb). Dense, shading vegetation reduces light resources, while lateral spread of rhizomes and roots reduces belowground regeneration opportunities. Seed germination and bud sprouting (solid black circles) are reduced and the capacity of the grassland to regenerate favors dominant plant species.

Abrahamson 2008). It would seem, then, that disturbance in grasslands must occur frequently, both spatially and temporally, for a range of subordinate and transient species to thrive.

However, gaps may not result in successful regeneration if propagule availability of subordinate species is limited. Accordingly, seed addition to disturbed vegetation (ie gaps) can increase plant species richness by up to 70% (Myers and Harms 2009). Forbs are usually more seed-limited than grasses, and increasing population size from seeds in grasslands is less likely for forb than for grass species (Turnbull *et al*. 2000). Seed limitation probably results from the interactions of several factors, including lower rates of pollination due to declines in pollinator diversity and abundance (eg Potts *et al*. 2016). A key driver of pollinator decline is reduced abundance of host plants (insect-pollinated plants such as forbs), where reduced seed set and associated forb decline represent growing threats to both subordinate forbs and their pollinators (Biesmeijer *et al*. 2006). Reductions in pollination and seed availability, therefore, are other important factors as to why forbs are subordinate in grasslands (Figure 3).

A fourth factor accounting for the lower abundance of forbs is access to sunlight (Figure 3). Several forb species are light dependent (Weigl and Knowles 2014) and therefore resource-limited if shaded by taller vegetation. In grasslands where the majority of species are forbs (Seabloom *et al*. 2013), a positive relationship between increased light availability (as a consequence of herbivory) and species richness was found (Borer *et al*. 2014). Furthermore, the recent synthesis of global grassland studies, revealing that plant species richness was higher in grasslands where herbivores reduced the abundance of dominant species (mentioned above), also indicates that light availability is a limiting factor (Koerner *et al*. 2018). Additional indirect evidence of light limitation comes from studies showing that N enrichment benefits the growth of grasses more than forbs (Wooliver *et al*. 2016); while plant species richness is declining in European grasslands in response to anthropogenic N deposition, sites with lower rates of N deposition have both higher species richness and higher proportions of forb species (Duprè *et al*. 2010). It can therefore be assumed that N deposition puts forb species at higher risk. However, plant species richness is also higher in fertilized grasslands where herbivory increases light availability (Borer *et al*. 2014) and in more productive grasslands where herbivory reduces plant species dominance (Koerner *et al*. 2018), suggesting that forbs are at a competitive disadvantage to other growth forms, particularly when light is a limiting factor.

In summary, we present three hypotheses for why forbs thrive in contemporary grasslands. First, regeneration gaps and access to sunlight that, in our interpretation, must have been common in the mammoth steppe appear to be key to developing and maintaining high forb species richness in present-day grasslands. Second, regeneration gaps likely promote forbs as long as propagules are not a limiting factor. Third, improved conditions for various guilds of forbs to establish, grow, and flower may trigger feedback loops, in which conditions for pollinators are improved, leading to higher rates of pollination and consequently enhanced forb seed production and abundance.

Conclusions

At a global level, forbs are the most species-rich, phylogenetically and functionally diverse growth form in grasslands. In addition, forbs rank high among grassland species in terms of primary productivity, nutrient content, production of anti-herbivory defenses, and tolerance to herbivory, and play a disproportionate role in influencing grassland function. Therefore, forbs are of central importance not only to the conservation of biodiversity within, and the functioning of, the grassland biome but also to its future sustainable management.

The consistent presence of forb species in grasslands from the Pleistocene to the present suggests that the conditions determining forb prevalence can potentially guide their conservation. We hypothesize that forbs thrived under the niche construction (sensu Odling-Smee *et al*. 2003) behaviors and activities of the megaherbivores that lived on the mammoth steppe, and that such niche construction may be essential for maintaining high species richness and productivity in present-day grasslands (eg Weigl and Knowles 2014). We further hypothesize that regeneration conditions and access to light – conditions also assumed to be the result of megafauna behaviors and activities in the mammoth steppe – are linked to higher species richness of forbs in contemporary grasslands.

We recommend that greater research and management effort be focused on the various guilds of forbs to conserve the biodiversity and functioning of the grassland biome worldwide. In particular, more attention should be given to the subordinate and transient forb species, their phylogenetic diversity and relevant functional groupings, and how conditions for promoting their survival, growth, and reproduction can be improved throughout the world's remaining grassland systems.

References

Armas C and Pugnaire FI. 2011. Belowground zone of influence in a tussock grass species. *Acta Oecol* **37**: 284–89.

Augustine DJ and McNaughton SJ. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *J Wildlife Manage* **62**: 1165–83.

Avolio ML, Forrestel EJ, Chang CC, *et al*. 2019. Demystifying dominant species. *New Phytol* **223**: 1106–26.

Bardgett RD and Wardle DA. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* **84**: 2258–68.

Barnosky AD, Hadly EA, Gonzalez P, *et al*. 2017. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* **355**: eaah4787.

Biesmeijer JC, Roberts SPM, Reemer M, *et al*. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**: 351–54.

Blinnikov MS, Gaglioti BV, Walker DA, *et al*. 2011. Pleistocene graminoid-dominated ecosystems in the Arctic. *Quaternary Sci Rev* **30**: 2906–29.

Bond WJ and Keeley JE. 2005. Fire as a global "herbivore": the ecology and evolution of flammable ecosystems. *Trends Ecol Evol* **20**: 387–94.

Bond WJ and Parr CL. 2010. Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. *Biol Conserv* **143**: 2395–404.

Borer ET, Seabloom EW, Gruner DS, *et al*. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* **508**: 517–20.

Bråthen KA and Ravolainen VT. 2015. Niche construction by growth forms is as strong a predictor of species diversity as environmental gradients. *J Ecol* **103**: 701–13.

Coppock DL, Detling JK, Ellis JE, *et al*. 1983. Plant–herbivore interactions in a North American mixed-grass prairie. *Oecologia* **56**: 1–9.

Coughenour MB. 1985. Graminoid responses to grazing by large herbivores – adaptations, exaptations, and interacting processes. *Ann Mo Bot Gard* **72**: 852–63.

Dirzo R, Young HS, Galetti M, *et al*. 2014. Defaunation in the Anthropocene. *Science* **345**: 401.

Duprè C, Stevens CJ, Ranke T, *et al*. 2010. Changes in species richness and composition in European acidic grasslands over the past 70 years: the contribution of cumulative atmospheric nitrogen deposition. *Glob Change Biol* **16**: 344–57.

Eilts JA, Mittelbach GG, Reynolds HL, *et al*. 2011. Resource heterogeneity, soil fertility, and species diversity: effects of clonal species on plant communities. *Am Nat* **177**: 574–88.

Eriksson O. 2013. Species pools in cultural landscapes – niche construction, ecological opportunity and niche shifts. *Ecography* **36**: 403–13.

Fahnestock JT and Detling JK. 2002. Bison–prairie dog–plant interactions in a North American mixed-grass prairie. *Oecologia* **132**: 86–95.

Fuhlendorf SD and Engle DM. 2004. Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. *J Appl Ecol* **41**: 604–14.

Gibson DJ. 2009. Grasses and grassland ecology. New York, NY: Oxford University Press.

Gibson DJ and Newman JA. 2019. Grasslands in the Anthropocene: research and conservation needs. In: Gibson DJ and Newman JA (Eds). Grasslands and climate change. Cambridge, UK: Cambridge University Press.

Grime JP. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J Ecol* **86**: 902–10.

Hawkes CV and Sullivan JJ. 2001. The impact of herbivory on plants in different resource conditions: a meta-analysis. *Ecology* **82**: 2045–58.

Johnson CN. 2009. Ecological consequences of Late Quaternary extinctions of megafauna. *P Roy Soc B-Biol Sci* **276**: 2509–19.

Kindscher K and Wells PV. 1995. Prairie plant guilds: a multivariate analysis of prairie species based on ecological and morphological traits. *Vegetatio* **117**: 29–50.

Klimešová J and Klimeš L. 2007. Bud banks and their role in vegetative regeneration – a literature review and proposal for simple classification and assessment. *Perspect Plant Ecol* **8**: 115–29.

Koerner SE, Smith MD, Burkepile DE, *et al*. 2018. Change in dominance determines herbivore effects on plant biodiversity. *Nat Ecol Evol* **2**: 1925–32.

Lennartsson T and Oostermeijer JGB. 2001. Demographic variation and population viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity. *J Ecol* **89**: 451–63.

Linder HP, Lehmann CER, Archibald S, *et al*. 2018. Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. *Biol Rev* **93**: 1125–44.

Massey FP, Ennos AR, and Hartley SE. 2007. Grasses and the resource availability hypothesis: the importance of silica-based defences. *J Ecol* **95**: 414–24.

McMillan BR, Pfeiffer KA, and Kaufman DW. 2011. Vegetation responses to an animal-generated disturbance (bison wallows) in tallgrass prairie. *Am Midl Nat* **165**: 60–73.

Murguzur FJA, Bison M, Smis A, *et al*. 2019. Towards a global arctic–alpine model for near-infrared reflectance spectroscopy (NIRS) predictions of foliar nitrogen, phosphorus and carbon content. *Sci Rep-UK* **9**: 8259.

Myers JA and Harms KE. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. *Ecol Lett* **12**: 1250–60.

Niinemets Ü, Keenan TF, and Hallik L. 2015. A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. *New Phytol* **205**: 973–93.

Odling-Smee FJ, Laland KN, and Feldman MW. 2003. Niche construction: the neglected process in evolution. Princeton, NJ: Princeton University Press.

Olff H and Ritchie ME. 1998. Effects of herbivores on grassland plant diversity. *Trends Ecol Evol* **13**: 261–65.

Owen-Smith N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology* **13**: 351–62.

Pokorny ML, Sheley RL, Svejcar TJ, *et al*. 2004. Plant species diversity in a grassland plant community: evidence for forbs as a critical management consideration. *West N Am Naturalist* **64**: 219–30.

Poorter H and Remkes C. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* **83**: 553–59.

Porensky LM and Veblen KE. 2015. Generation of ecosystem hotspots using short-term cattle corrals in an African savanna. *Rangeland Ecol Manag* **68**: 131–41.

Potts SG, Imperatriz-Fonseca V, Ngo HT, *et al.* 2016. Safeguarding pollinators and their values to human well-being. *Nature* **540**: 220–29.

Reich PB, Tilman D, Isbell F, *et al.* 2012. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* **336**: 589–92.

Romero GQ, Gonçalves-Souza T, Vieira C, *et al.* 2015. Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biol Rev* **90**: 877–90.

Sage RF. 2004. The evolution of C_4 photosynthesis. *New Phytol* **161**: 341–70.

Sandom C, Faurby S, Sandel B, *et al.* 2014. Global late Quaternary megafauna extinctions linked to humans, not climate change. *P Roy Soc B-Biol Sci* **281**: 20133254.

Seabloom EW, Borer ET, Buckley Y, *et al.* 2013. Predicting invasion in grassland ecosystems: is exotic dominance the real embarrassment of richness? *Glob Change Biol* **19**: 3677–87.

Siebert F and Dreber N. 2019. Forb ecology research in dry African savannas: knowledge, gaps, and future perspectives. *Ecol Evol* **9**: 7875–91.

Siebert F and Scogings P. 2015. Browsing intensity of herbaceous forbs across a semi-arid savanna catenal sequence. *S Afr J Bot* **100**: 69–74.

Strauss SY and Agrawal AA. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends Ecol Evol* **14**: 179–85.

Strauss SY, Rudgers JA, Lau JA, *et al.* 2002. Direct and ecological costs of resistance to herbivory. *Trends Ecol Evol* **17**: 278–85.

Turnbull LA, Crawley MJ, and Rees M. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* **88**: 225–38.

Uys RG, Bond WJ, and Everson TM. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biol Conserv* **118**: 489–99.

Veldman JW, Buisson E, Durigan G, *et al.* 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. *Front Ecol Environ* **13**: 154–62.

Vicari M and Bazely DR. 1993. Do grasses fight back? The case for antiherbivore defences. *Trends Ecol Evol* **8**: 137–41.

Waldram MS, Bond WJ, and Stock WD. 2008. Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. *Ecosystems* **11**: 101–12.

Wang L, Wang D, Liu J, *et al.* 2011. Diet selection variation of a large herbivore in a feeding experiment with increasing species numbers and different plant functional group combinations. *Acta Oecol* **37**: 263–68.

Weigl PD and Knowles TW. 2014. Temperate mountain grasslands: a climate–herbivore hypothesis for origins and persistence. *Biol Rev* **89**: 466–76.

Weisser WW, Roscher C, Meyer ST, *et al.* 2017. Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: patterns, mechanisms, and open questions. *Basic Appl Ecol* **23**: 1–73.

Willerslev E, Davison J, Moora M, *et al.* 2014. Fifty thousand years of Arctic vegetation and megafaunal diet. *Nature* **506**: 47–51.

Wise MJ and Abrahamson WG. 2008. Applying the limiting resource model to plant tolerance of apical meristem damage. *Am Nat* **172**: 635–47.

Wooliver R, Pfennigwerth AA, Bailey JK, *et al.* 2016. Plant functional constraints guide macroevolutionary trade-offs in competitive and conservative growth responses to nitrogen. *Funct Ecol* **30**: 1099–108.

Yurtsev BA. 2001. The Pleistocene "tundra–steppe" and the productivity paradox: the landscape approach. *Quaternary Sci Rev* **20**: 165–74.

Zimov SA, Chuprynin VI, Oreshko AP, *et al.* 1995. Steppe–tundra transition – a herbivore driven biome shift at the end of the Pleistocene. *Am Nat* **146**: 765–94.

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