Grassland Communities and Ecosystems

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Abstract

Grasslands represent one of the largest vegetation types on Earth and their existence is determined by soil-water scarcity that in turn depends on precipitation and temperature. This vegetation type harbors a high diversity of plant species that mostly occurs at fine spatial scales because grasslands tend to be structurally simpler at coarser scales. Grassland species richness has strong and positive effects on primary production as a result of increasing niche complementarity with increasing diversity. Grasslands are among the most vulnerable ecosystems in the world because their diversity is threatened by human activity, mostly as a consequence of conversion into croplands.

Glossary

Convention on biological diversity The Convention was first enacted in June 1992, has been signed by many countries, and its objectives are the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources, including by appropriate access to genetic resources and by appropriate transfer of relevant technologies, taking into account all rights over those resources and to technologies, and by appropriate funding.

Functional type A group of species that share morphological and physiological characteristics that result in a common ecological role.

Niche complementarity Refers to how the ecological niches of species may not fully overlap and complement each other. Consequently, an increase in the number of species that complement each other may result in a larger volume of total resources utilized and in higher rate of ecosystem processes.

Sampling effect Refers to the phenomenon where increases in the number of species increase the probability of including in the community a species with a strong ecosystem effect (Huston, 1997). This phenomenon yields an increase in ecosystem processes with increases in diversity without invoking niche complementarity.

Biodiversity scenarios Scenarios of biodiversity (Sala *et al.*, 2000) depict alternative future paths for biodiversity at different temporal and spatial scales. Scenarios are driven by global change drivers (Flombaum *et al.*, 2017) that include climate, land-use change, species invasions and direct CO_2 effects. Scenarios are not meant to forecasting the future but identifying consequences of changes in drivers on future biodiversity.

Key Points

- Grasslands, one of the largest vegetation types on Earth, are dominated by grasses and occur in regions with soil-water deficit.
- Grasslands are rich in plant diversity at fine spatial scales but tend to be poorer at large spatial scales.

- A distinctive feature in grassland fauna is the presence of large grazing mammals.
- Grasslands played a key role in testing the biodiversity-ecosystem-functioning hypothesis a central focus in ecology in the context of biodiversity change.
- Grassland ecosystems are threatened in the context of global change by human activities, and 30% of their biota is estimated to be extinct or threatened.

Introduction

Grasslands are key for human wellness and are largely modified by human activities. This article explores the occurrence and biodiversity of grasslands in the context of global change. The questions to address are, first, what climatic and edaphic characteristics determine the extension this natural vegetation type. Second, what are the most relevant features of grasslands biodiversity, with focus on plants, animals and soil microbes. Third, what is the relationship between plant diversity and ecosystem functioning, and which are the major mechanisms explaining this relationship. Last, what are the major changes in biodiversity expected for this ecosystem. In this way, the article provides a synthesis of this natural ecosystems, and the causes and consequences of change in its diversity.

Extent of Grasslands

Grasslands are one of the major vegetation types in the world accounting for more than 30% of terrestrial surface, with an estimated range of 31%–43% depending on different classifications (Shantz, 1954). Grassland vegetation is dominated by herbaceous plants, mostly grasses (Poaceae), and varying proportion of woody species. They exist in all continents and cover a vast area of 41--56 $\times$ 10^6 km^2. In North America, grassland is the potential natural vegetation of most of the Great Plains and it reaches from the Chihuahuan desert in the south to the deciduous forests of Canada in the north, and from the Rocky Mountains in the west to the deciduous forest of the eastern United States (Fig. 1). In South America, grassland is the potential vegetation of the vast pampas and most of the Patagonian steppe. Finally, in Asia, grassland ecosystems cover a huge area from Ukraine to China.

This article focuses on grasslands which include grass-shrubs deserts and grasslands, and excludes savannas. It also excludes grasslands resulting from human intervention. These anthropogenic grasslands are located in areas where potential natural vegetation is forest. Humans, in an attempt to produce forage for domestic animals, have logged forests and have maintained these plots as grasslands by mowing them periodically. Selective grazers and mowing also control the distribution of grasslands. A large fraction of European grasslands would not be grasslands if it was not for the frequent mowing.
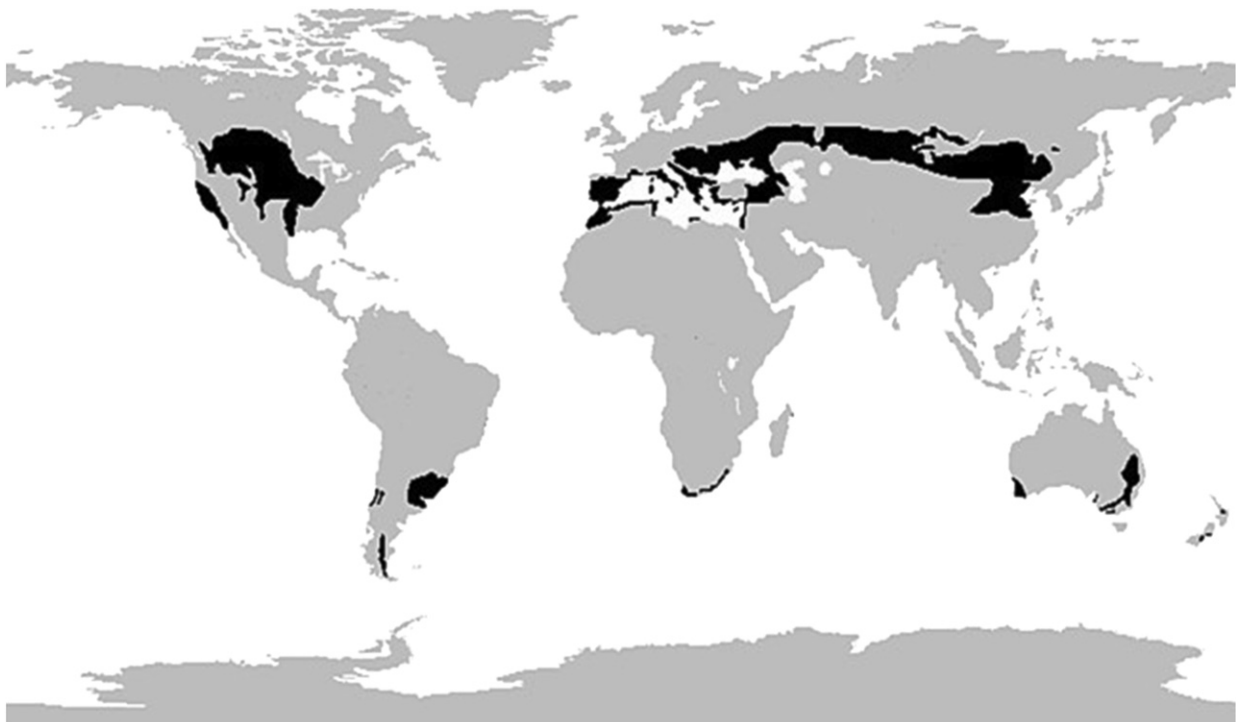

Fig. 1   Map of the global distribution of temperate grasslands. Adapted from Figure 7.2 in Bailey (2014). Ecoregions: The ecosystems geography of the oceans and continents, 87 New York: Springer.
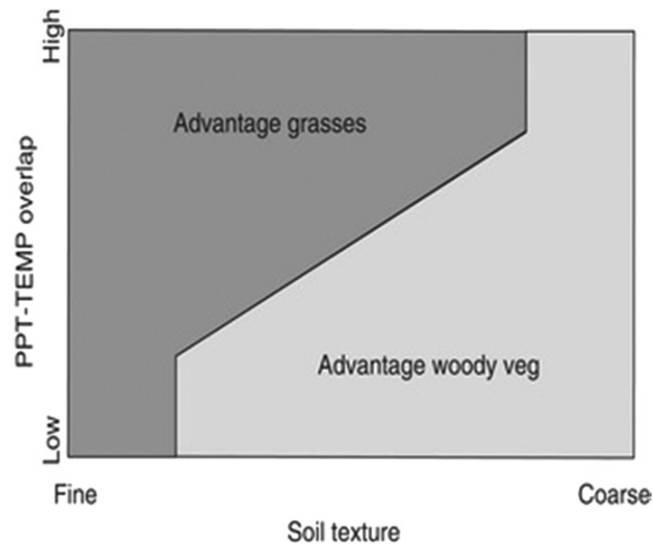
Fig. 2 A conceptual model explaining the relative abundance of grasses and woody vegetation as a function of overlap in seasonality of temperature and precipitation (congruence of warm and wet seasons) and soil texture. The darker area represents conditions that are likely to favor the persistence of grasses, while the lighter area represents conditions that favor woody vegetation. The intersection of the two areas represents points where biotic influences are likely to be most pronounced. Adapted from Sala, O.E., Lauenroth, W.K. and Golluscio, R.A. (1997). Plant functional types in temperate semi-arid regions. In: Smith, T.M., Shugart, H.H. and Woodward, F.I. (eds) Plant functional types, pp. 217–233. Cambridge: Cambridge University Press.

Determinants of Grasslands

Grasslands are water-limited ecosystems, and soil-water availability defines their distribution in space. The amount of water available for plants primarily depends on precipitation amount and temperature. The former is the input of water and the latter controls the loss of water from the ecosystem, since as temperature increases so does the evaporative demand. Increases in temperature result in increases in soil evaporation and plant transpiration; consequently, for a similar precipitation regime, the water balance becomes more negative as temperature increases. In contrast with most biological phenomena, primary production in grasslands decreases with increasing temperature, highlighting the importance of the indirect mechanism of the temperature control on the distribution of grasslands (Epstein *et al.*, 1996).

Grassland ecosystems mostly occur in areas of the world that have an annual precipitation between 150 and 1200 mm and mean annual temperature between 0 and 25°C (Whittaker, 1975). Along precipitation gradients grasslands are located between forests and deserts. In North America, South America and Asia, clear E–W precipitation gradients exist. In North and South America there are very small changes in elevation along those precipitation gradients and vegetation changes are mostly accounted for by precipitation. At the eastern and wettest end of North America, tallgrass prairie is the dominant vegetation, which is replaced by mixed-grass prairie and by shortgrass steppe at the driest end of the gradient. A similar pattern occurs in Asia and South America (Fig. 1).

Although temperature and precipitation are the major determinants of the distribution of grasslands, fire also may play an important role. Fire becomes particularly important in the grass–forest ecotones where the dominance of grasses or woody plants in many cases is determined by the frequency and intensity of fires. For example, in North American tallgrass prairie, the area covered by woody plants has increased dramatically in the past 100 years and the human intervention in reducing fire frequency is largely responsible for the change (Briggs *et al.,* 1998). Similarly, data from pollen profiles, tree ring analysis, and photographic sources documented a shift in the grassland–forest ecotone in northern Patagonia with woody vegetation invading grasslands (Veblen and Markgraf, 1988). Again, fire control implemented by land managers was apparently responsible for the forest expansion.

Soil texture also modulates the distribution of grasslands by modifying the soil water-holding capacity and the location of water in the profile. First, water penetrates deeper into the soil profile in coarse-textured soils than in fine-textured soils. This is because soil water-holding-capacity is lower in coarse- than fine-textured soils. Therefore, the same rainfall event penetrates deeper in a coarse- than in a fine-textured soil. Second, grasses and woody vegetation have contrasting rooting patterns with grasses having predominantly shallow roots and shrubs and woody plants having deep roots (Jackson *et al.*, 1996). Consequently, for a given amount of precipitation, grasses dominate in areas with predominantly fine-textured and woody-plants in coarse-textured soils (Sala *et al.,* 1997, Fig. 2).

Finally, seasonality of precipitation and the synchrony between the wet and warm seasons also affect the dominance of grasses and woody vegetation. Regions such as the Patagonian grasslands in South America, where precipitation occurs during the cold season when evapotranspiration is low, experience a deep distribution of water in the soil profile (Paruelo and Sala, 1995, Fig. 2). In these types of ecosystems, because during the rainy season temperature and evaporation are low, each rainfall event is likely to find a wet soil with upper soil horizons water saturated. Therefore, after a precipitation event water penetrates deeper into the soil profile. In contrast, in regions with similar total precipitation but occurring during the warm

season, such as the shortgrass steppe in North America, the profile of soil water availability is shallow (Sala *et al.*, 1992). Evapotranspiration in between rainfall events is high so each rainfall event most likely finds a dry soil profile consequently just wetting the uppermost horizons. In synthesis, for equal amounts of annual precipitation, ecosystems with cold season precipitation tend to have deeper soil water profiles and have a higher component of woody plants. Ecosystems with warm season precipitation tend to have shallower soil water profiles and are dominated by grass vegetation.

The grassland-forest ecotone seems quite dynamic and driven by climate and land-use change. Hirota *et al.* (2011), using satellite information, have shown that woody-plant abundance changes abruptly along precipitation gradients. Instead of a gradual increase in woody plant abundance with precipitation they observed an abrupt transition as ecosystems tend to exist in either the grass dominated realm or the wood-plant domain. Climate change and the associated warming in South America is expected to decrease forest area while increasing tree-less and savannas (Anadón *et al.*, 2014). Agriculture expansion has also occurred in the forest-grassland ecotone where there is enough precipitation to sustain dryland agriculture.

The dynamics of the grassland-desert or grassland-woodland ecotones seem to be driven by invasive species expansions. Archer *et al.* (2017) have described how conspicuous woody-plant invasions are across all continents and grasslands types. The ultimate driver or drivers of this phenomenon are still debated and include changes in climate, fire regime, grazing intensity and CO_2.

Biodiversity

Biodiversity can be examined in many different ways, and multiple definitions exist for what constitutes "biodiversity". Here, we focus on biodiversity in terms of taxonomically defined species for plants and animal, and for microbial diversity in terms of "operational taxonomic units" (OTU) since the vast majority of studies quantifying ecosystem variation have used this measure. OUT refer to DNA sequence similarity which is used to assign microbial individuals to different taxonomic level. However, genetic biodiversity (genetic variation within a single species) and ecological diversity (including landscape diversity and functional group diversity) are also important components of biological diversity (Brondízio *et al.*, 2019). The definition of biodiversity, therefore, depends to a certain extent on scale of interest, as well as the size of the organisms.

Diversity of Plants

Floristic diversity in grasslands varies broadly, with many natural types of grassland having a very high level of plant species diversity, at times approaching that seen in mainland tropical forests (Groombridge and Jenkins, 2002). Grasslands are dominated by grasses (family Poaceae, excluding bamboos). The pampa region in Argentina represents some of the highest diversity grassland, with more than 400 species of grasses (Cabrera, 1970). Similar numbers can be found in the tallgrass prairie of North America (Freeman, 1998; Wilsey *et al.*, 2005), the vast majority of which are perennial grasses that can still be found in remnant sites.

Plant species diversity shows a great spatial variation. Grassland communities can be very species rich at fine spatial scales but tend to be similar and structurally simple over large areas (Groombridge and Jenkins, 2002). For example, plant-species turnover among stands occupying different landscape positions was 50% greater than among communities encompassing two degrees of latitude in the Flooding Pampa grasslands of Argentina (Perelman *et al.*, 2001). Grasslands tend to have low rates of endemism, however, and the climatic and soil gradients within them have led to ecotypic variation and high genetic diversity (Groombridge and Jenkins, 2002). Plant species of grasslands can be categorized into four functional types: grasses, shrubs, succulents, and herbs (Sala *et al.*, 1997). The classification of plant species into functional types only has epistemological value and serves the purpose of facilitating the study and management of grasslands. This classification can be divided into many new subcategories or aggregated into fewer units depending on the needs of the analysis.

Grassland plant species can also be classified according to their photosynthetic pathway into C_3 and C_4 species. The two groups of species have differences in the physiology of photosynthesis and in the morphology of leaves that result in different ecological characteristics that separate them in time and space. Regional analyses of the distribution of these two types of grass species showed that C_3 species decrease southward in North America and northward in South America and C_4 species show the opposite pattern. Similarly, the abundance of C_3 species increases whereas that of C_4 decreases along an altitudinal gradient (Cavagnaro, 1988). These biogeographical analyses correlate with ecophysiological studies showing that C_4 species have photosynthesis optima at higher temperature, have higher water use efficiency, and are better adapted to low water availability conditions (Kemp and Williams, 1980).

Diversity of Animals

All major taxonomic groups are represented in grasslands, but despite their large areal extent (40% of the area of terrestrial ecosystems), overall faunal diversity is lower than in many other biomes. The number of bird and mammalian species that are found primarily in grasslands are estimated to be 477 and 245, respectively, representing only 5% of the world's species for each taxonomic group (Groombridge, 1992). Local diversity can be high in specific areas. For example, there are an estimated 208 avian species for tallgrass prairie (Kauffman *et al.*, 1998). However, general patterns show lower diversity for most taxonomic groups compared with other ecosystems.

One of the striking features of grasslands in terms of animal diversity is the presence of large herbivores as a prominent component of secondary production. These large grazing mammals have an important impact on the functioning of grasslands, altering patterns of nutrient cycling, primary production, and plant species composition (McNaughton, 1993), although their presence and diversity varies across different continents. For example, in the Great Plains of North America, nearly all the large grazing mammals went extinct during the glaciation of the Pleistocene, but the proliferation of a very few species, particularly *Bison* (plains bison), dominated the plant-herbivore interactions until the introduction of domestic cattle at the beginning of the twentieth century (Lauenroth and Milchunas, 1992). In contrast, African grasslands contain very high level of mammalian diversity of grazers, with up to 20 species coexisting in a single reserve (Cumming, 1982). Finally, many South American grasslands evolved without the presence of large grazers, and their primary herbivory prior to the introduction of sheep and cattle was due to insect species (Bucher, 1982). Thus, although there is variation in the diversity of the large herbivores, their presence and importance are a distinctive characteristic of grassland ecosystems.

Small mammals, birds, reptiles, amphibians, and insects also play an important role in the functioning of grasslands. Species richness of small mammals is actually higher than that for large mammals (168 versus 77 species overall), and they are mostly granivores or omnivores (Groombridge, 1992). In contrast, in Australian deserts small mammals are mostly insectivorous. Fluctuations in seed supply caused by unpredictable environmental conditions and the infertile soils could be an explanation for these differences (Morton, 1993).

Avian diversity in grasslands represents 5% of the total species of the world species number, and again the fluctuating climate has an important control on this distribution. In this case, birds can migrate to remote areas outside of the grassland biome to seek alternative resources in periods of unfavorable conditions. In North American grasslands, which have a strong seasonality, there are large annual variations of passerines in response to climatic conditions. Additionally, within the grassland ecosystems, there exists a gradient of avian biomass that decreases with precipitation and primary production from the tallgrass prairie to the mixed-grass prairie and shortgrass steppe (Lauenroth and Milchunas, 1992). Yet, human alteration in this ecosystem resulted in a 74% decline of breeding species populations, the largest declined reported across North American biomes (Rosenberg et al., 2019). Reptiles in grasslands are less diverse than mammals and birds, and amphibians are less diverse than reptiles in the tallgrass prairie of North America (Kauffman et al., 1998). Latitude has an effect on the diversity of reptiles and amphibians because they are ectothermic organisms, with an increase in the number of species from north to south of the tallgrass prairie (Kucera, 1992).

Insects are a diverse element of the terrestrial macrofauna of tallgrass prairie (Kauffman et al., 1998), reflecting general patterns of diversity for terrestrial ecosystems in which insects represent more than 50% of the species (Strong et al., 1984). They have a very important role as herbivores, pollinators, predators, parasitoids, and decomposers. Herbivorous insects are probably the most conspicuous functional group in tallgrass prairie (Kauffman et al., 1998) and may replace large grazing mammals as the primary consumer in some South American grasslands (McNaughton et al., 1993). Arthropods, constituting the largest proportion of invertebrates in the shortgrass steppe and primarily herbivores, take advantage of the large amount of belowground primary production (Lauenroth and Milchunas, 1992). In fact, most grassland invertebrate biomass is found within the soil and may be in the order of 100–1000 times as great as vertebrate biomass (Groombridge and Jenkins, 2002).

Diversity of Soil Biota

Grasslands harbor an enormous diversity of soil biota that live all or part of their lives in or on the soil. Soil microorganisms are broadly defined as a group of microscopic life forms that include bacteria, archaea, viruses, and eukaryotes like fungi. Soil animals comprise protozoa and nematodes (conventionally grouped as microfauna because of their micrometric size), springtails, mites and other microarthropods (mesofauna, mm), and earthworms, termites, ants, beetles, and millipedes, among others (macro-fauna, cm). Yet, a clear understanding of soil biodiversity is still lacking compared to that of plants and animals because their tiny size and hidden existence challenge their study (Wall et al., 2010).

Microbial diversity has become tractable thanks to the development of molecular biology, providing opportunities to understand soil biodiversity with special insights for grasslands (Fierer et al., 2009). A single gram of soil can contain 10,000--50,000 different microbial organisms (Roesch et al., 2007), but because so few of them have been described, similar organisms are grouped within OTU. At the global scale, soil bacterial and fungal diversity is primarily controlled by soil pH and mean annual precipitation (Lauber et al., 2009; Tedersoo et al., 2014). A study conducted across drylands that included grasslands and shrublands of all continents revealed that the diversity and abundance of soil bacteria and fungi was primarily affected by aridity (Maestre et al., 2015). The effects of aridity were directly associated with reductions in soil organic matter, which in turn is strongly related to microbial biomass (Fierer et al., 2009; Maestre et al., 2015). Thus, the importance of soil pH as a driver of microbial diversity reported across biomes is not apparent in those water-limited ecosystems where soil pH is generally close to neutral.

Diversity of soil bacteria in drylands is dominated by five bacterial phyla (Acidobacteria, Actinobacteria, Bacteroidetes, Proteobacteria, and Verrucomicrobia). Diversity of soil fungi is dominated by phyla Ascomycota and Basidiomycota (Fierer et al., 2012; Tedersoo et al., 2014). In native tallgrass prairie of United States, a reconstruction of the soil microbial communities that once existed prior to agricultural practices revealed that changes in the relative abundance of Verrucomicrobia drove the biogeography of bacterial communities, with more than 50% abundance in the center of Tallgrass Prairie distribution but less than 15% on the edges of the prairie range (Fierer et al., 2013). In xeric grasslands and shrublands, aridity shifted the relative abundance of main bacterial phyla: Acidobacteria and Verrucomicrobia decreased, and Chloroflexi and increased α-Proteobacteria (Maestre et al., 2015). Little is known,

yet, about the implication of bacterial biogeographic patterns on ecosystem functioning, but microbial traits provide the necessary link between microbial community composition and soil ecosystem functioning (Martiny et al., 2015).

Soil fungi can be classified by functional groups based on how they get their energy: saprotrophs (dead organic matter), mycorrhiza (colonize roots and obtain carbon from plants and, in exchange, help solubilize phosphorus and bring soil nutrients to plants), and pathogens (reduced production or death when they colonize roots and other organisms). All these functional groups are present in grasslands, but they have a low proportion (11.9%) of ectomycorrhizae, which is a particular type of mycorrhizae that grows on the surface layers of the roots, compared to other biomes (Tedersoo et al., 2014). In contrast, the number of endomycorrhizae that grows within the root cells per host plant species is high in grasslands (8.3 fungal taxa per plant species) and is only outnumbered in tropical forests (18.2 fungal taxa per plant species (Öpik et al., 2006)). These results highlight the tight association between fungal communities and vegetation types.

One special feature of grassland microbiota, particularly in xeric areas with low plant cover, is the presence of biological soil crusts. They are complex microbial communities that build crusts on the top layer of arid soils (Garcia-Pichel and Belnap, 1996; Belnap, 2003). Biological soil crusts are dominated by Cyanobacteria (e.g., Microcoleus sp.), a particular group that obtains energy through photosynthesis and produce a high amount of slime (extra-polymeric substances) that traps mineral particles and contribute to the formation of the crust. This Cyanobacteria species also produces large quantities of metabolic compounds capable of reducing soil surface albedo, and consequently increasing soil surface temperature (Couradeau et al., 2016). Other members of the crust are bacteria, lichens, eukaryotic microalgae, and mosses. Biological crusts contribute to carbon and nitrogen fixation in these ecosystems, help stabilize soil against erosion, and modify soil-surface temperature.

Soil fauna is another important component of grasslands soils. Their biomass represent 4% of microbial biomass in grasslands, a higher proportion than the 2% global average (Fierer et al., 2009). The relative importance in terms of biomass of the different groups within soil fauna is Earthworms > Enchytraeids > Nematoda > Acari > Collembola (Fierer et al., 2009). The size of these organisms can restrict their location in the soil habitat. Smaller members of the microfauna like nematodes are basically aquatic organisms that live in the thin water films or capillary pores of aggregates, preying or grazing on other aquatic microfauna. Thus, soil nematodes abundance is closely related to soil moisture in mesic grasslands (Sylvain et al., 2014). However, soil nematodes abundance was unaffected by increased or decreased soil moisture in xeric grasslands, suggesting that other factors impose a larger control on nematode abundance in ecosystems with strong water limitation (Sylvain et al., 2014; Vandegehuchte et al., 2015). The trophic structure of soil microorganisms seems to be controlled by soil water with larger predators being the most sensitive to changes in soil water (Ankrom et al., 2020; Franco et al., 2019). In terms of species numbers, a soil invertebrate study in tallgrass prairie showed more than 200 species of nematodes, with fungivores constituting 40% of the nematode species and the nematode biomass was exceeded only by that of bacterial and fungal groups (Ransom et al., 1998).

Biodiversity and Ecosystem Functioning in Grasslands

The hypothesis about the relationship between biological diversity and the functioning of ecosystems has been central in ecology; and grassland ecosystems have been crucial in testing it. The biodiversity and ecosystem functioning hypothesis indicates that the rate of ecosystem processes, such as primary productivity or nutrient cycling, increases as species richness increases and that this relationship eventually saturates (Vitousek and Hooper, 1993). The increase in ecosystem functioning can be interpreted as an evidence of niche complementarity; that is, the higher the number of species with niches that do not overlap the larger the total volume of resources exploited (Tilman et al., 1997). For example, plots containing just shallow-rooted or deep-rooted species should have lower productivity than plots containing both groups of species that jointly have access to water and nutrients stored in both upper and lower layers of the soil. Alternatively, the same relationship was interpreted as a result of the increased probability of including species that outperform the others as the number of species in the mix increases, known as the sampling effect (Huston, 1997; Tilman et al., 1997).

Grassland ecosystems played a key role in testing the biodiversity-ecosystem-functioning hypothesis mostly because of the small size and short life span of grasses that made manipulative experiments feasible with few resources and in short periods of time. The most common manipulative experiment type that was used in grasslands is called "replacement series" where, at the beginning of the experiment, treatments differ in the number of species but keep plant biomass or density constant. This type of experiment normally includes treatments where each individual species grow alone. Monocultures are used to estimate biodiversity effect, that is the difference in production between full diversity and monoculture treatments (de Wit and van den Bergh, 1965; Loreau and Hector, 2001). The first large-scale field experiment was located in the North American tallgrass prairie and showed a saturating curve of total plant cover and nutrient uptake increasing with species richness up to a level of approximately 10 species (Tilman et al., 1996). Other sets of experiments across North and South America basically showed similar results (Reich et al., 2004; Flombaum and Sala, 2008).

Biodiversity also contributes to maintaining long-term stability of primary production in grasslands. Experiments maintained through more than a decade showed positive effect of biodiversity on the stability of primary production (Cardinale et al., 2013; Hautier et al., 2015; Isbell et al., 2015) A high stability in productivity means that the amount of biomass produced is similar among years and imposes a buffer effect against climatic variability. These experiments also show the positive effect of biodiversity on primary production persisted over time and were accompanied by an increase in niche complementarity (Reich et al., 2012). It is likely that the magnitude of the biodiversity effect is positively related to the co-evolutionary history of species in the mix and negatively to the frequency and intensity of disturbance (Sala, 2001), both most likely to occur in natural than in synthetic communities, and in long term than short term experiments.

A large effort has been made in identifying the relative contribution of niche complementarity and sampling effect. Using analytical tools, Loreau and Hector (2001) found that niche complementarity was the most important mechanism to account for increases in primary production with biodiversity. Long-term field experiments in grasslands further strengthened this argument by showing that niche complementarity increased while sampling effect decreased through time (Fargione et al., 2007; Van Ruijven and Berendse, 2009).

Niche complementarity can be assessed by the degree of overlap among species traits that affect resource use. In Patagonian grasslands, dominant plant species differed in resource use, and plant traits affecting water and nitrogen cycles contributed the most to niche complementarity (Flombaum and Sala, 2012). After more than two decades from the first experiments performed in grasslands, a general consensus exists that the positive relationship between plant diversity and net primary production is mostly due to niche complementarity (Hooper et al., 2005; Balvanera et al., 2006; Cardinale et al., 2007; Hillebrand and Matthiessen, 2009).

Comparison of multiple grassland experiments that manipulated several global-change drivers revealed that the loss of biodiversity imposed changes on primary production comparable to other stressors such as fire, N-deposition, grazing, or climate change (Tilman et al., 2012; Flombaum et al., 2017). Similarly, a metanalysis of experiments across world grasslands that explored the effects of global-change drivers on primary production showed that observed diversity change had comparable effects than other drivers (Emmett Duffy et al., 2017). Consequently, expected global biodiversity loss may have a negative effect on grasslands primary production and carbon sequestration.

Biodiversity Change in Grasslands

Biodiversity in grassland ecosystems is seriously threatened by human activity as assessments of current conditions and modeling of future scenarios reported. Assessments of biodiversity loss in grassland ecosystems indicated that 30% of species are threatened or extinct, similar to the global average (Isbell et al., 2022). Yet large uncertainty remains in this number ranging from 15 to 45%, that includes taxonomical and geographical biases and lack of information on threatened and extinct species. Two independent scenario studies developed at the global scale for the next 50 and 100 years highlighted that grassland ecosystems were among the most vulnerable ecosystem types (Sala et al., 2000, 2005). Depending on how interactions among drivers of biodiversity loss were modeled, grasslands ranged from the most threatened biome to the third most threatened behind tropical forests, arctic ecosystems, and southern temperate forests (Sala et al., 2000). According to the most comprehensive regional scenarios, grassland habitats will be degraded in a way that between 8% and 10% of its vascular plant species will be committed to extinction by the year 2050 (Sala et al., 2005). There is a lag from the time that habitat destruction occurs driving populations below the long-term survival size and the actual occurrence of species extinction (Cronk, 2016).

Grassland biodiversity loss occurs when: (1) big portions of these ecosystems disappear or (2) when they maintain their identity but are degraded. See discussion above about in the "Determinants of Grasslands" section how grassland ecotones have and will change as a result of land-use and climate change. Overexploitation includes the harvesting of species from the wild at a rate that exceeds the ability of regrowth of natural populations (Maxwell et al., 2016). Land-use change is mostly driven by the transformation into croplands and cultivated forests. What makes biodiversity in grassland ecosystems so vulnerable to human impact? Are grassland ecosystems particularly sensitive? Or, are they located in areas that will be affected the most? Grasslands are located in parts of the world where ecosystems are going to be hit the hardest by human activity (Sala et al., 2000, 2005). Grasslands are among the biomes that are going to experience the largest conversion in land use because of their mild climate and favorable soil conditions that made them quite suitable for agriculture. The most dramatic changes in land use in grasslands are those that result from conversion into croplands. The conversion into agricultural land is driven by patterns of population growth and agricultural efficiency, yet land use regulation and consumption preferences can also play a relevant role (Stehfest et al., 2019). Land conversion is not expected to be even across the world, for example, the IMAGE 3.0 model predicts for the year 2100 increases in agricultural area in Africa and decreases in area in North America (Doelman et al., 2018). Biodiversity losses resulting from conversion to agriculture in one part of the world are not offset by a similar area that will be abandoned and is now reverting to grassland but that is located in a different part of the world. Therefore, total change in grassland area underestimates the impact of land-use change on biodiversity.

Conclusion

Grassland ecosystems provide abundant wealth and benefits to humans, but human utilization of grasslands have a negative impact on their biodiversity. Societal demands and scientific advancement are key to achieve a sustainable use of grasslands.

Change History

This new version has multiple changes. The title, the first two sections present a more accurate definition of the scope of this article, the temperate grasslands. The section on diversity of soil biota has been drastically modified by adding an in depth view of the different groups of soil microorganisms and the variables that control their abundance. The section on the impacts of biodiversity on ecosystem functioning has been updated reflecting the quick pace of this field on inquiry. Finally, the section of the changes in grassland biodiversity has been updated to reflect past and future grassland biodiversity trends and scenarios for the coming decades and century.

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