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Grassland Ecosystems

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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.

Global biodiversity assessment (GBA) The Global Biodiversity Assessment is an independent peer-reviewed analysis of the biological and social aspects of biodiversity commissioned by United Nations Environment Programme.

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. *See* Functional Diversity chapter (00061) in this work for ways of distinguishing between niche complementarity and sampling effect.

Extent of Grasslands

Grasslands are one of the major vegetation types in the world accounting for almost 40% of terrestrial surface (Shantz, 1954). They exist in all continents and cover a vast area of 49×10^6 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 (Figure 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.

Determinants of Grasslands

Grasslands are water-limited ecosystems, and 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 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, Tall-grass 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 (Figure 1).
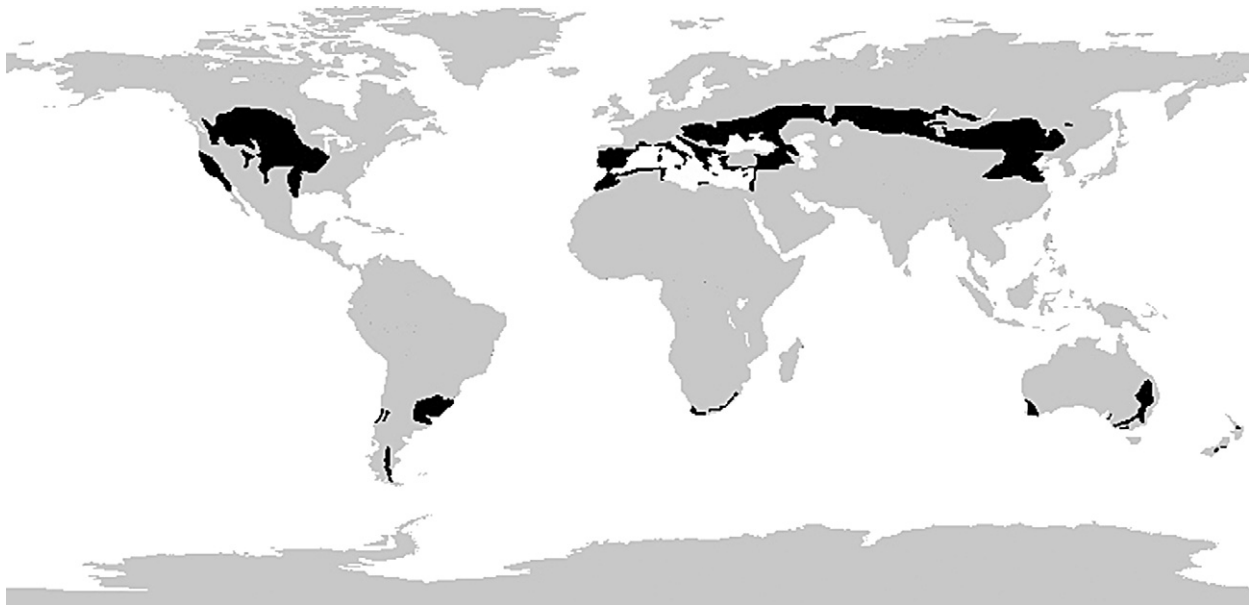
Figure 1   Map of the global distribution of temperate grasslands. Adapted from Figure 7.2 in Bailey RG (1998) *Ecoregions: The Ecosystems Geography of the Oceans and Continents*, 87 pp. New York: Springer.

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 Tall-grass 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 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 because soil water-holding-capacity depends on soil texture and is lower in the former. Therefore, the same rainfall event would penetrate 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 soils (Sala *et al.*, 1997) (**Figure 2**). Finally, seasonality of precipitation and the synchrony between the wet and warm seasons also affect the dominance of grasses and woody vegetation. Locations where precipitation occurs during the cold season, when evapotranspiration is low, result in a deeper distribution of water in the soil profile and these locations would benefit woody vegetation over grasses (**Figure 2**). In synthesis, precipitation and temperature are the major drivers
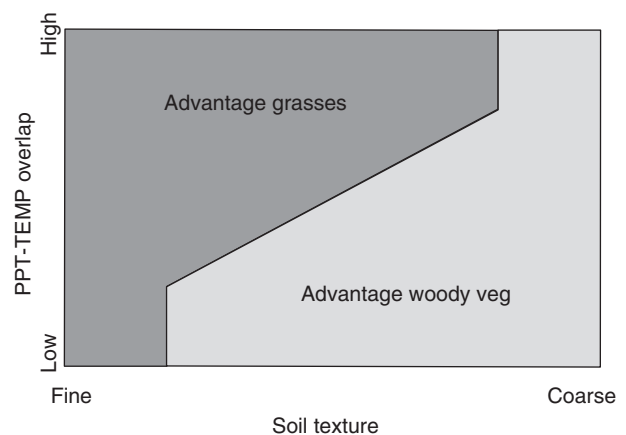

Figure 2   A conceptual model explaining the relative abundance of grasses and woody vegetation as a function seasonality of temperature and precipitation (congruence of warm and wet seasons) and soil texture. The gray shaded area represents conditions that are likely to favor the persistence of grasses, while the speckled 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 OE, Lauenroth WK, and Golluscio RA (1997) Plant functional types in temperate semi-arid regions. In: Smith TM, Shugart HH, and Woodward FI (eds.) *Plant Functional Types*, pp. 217–233. Cambridge: Cambridge University Press.

of the distribution of grasslands with their distribution modified at the edges by fire, soil and seasonality of precipitation.

This article focuses exclusively on climatically determined grasslands, in contrast with grasslands resulting from human intervention. 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.

Biodiversity

Biodiversity can be examined in many different ways, and multiple definitions exist for what constitutes "biodiversity." Nevertheless, the authors of the Global Biodiversity Assessment, using definitions originally proposed by the Convention on Biological Diversity, defined biological diversity as "variability among living organisms from all sources" (Heywood and Baste, 1995). Here, we focus on biodiversity in terms of taxonomically defined species, and the vast majority of studies quantifying ecosystem variation have used this measure. 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. The definition of biodiversity, therefore, will depend to a certain extent on one's objective and scale of interest, ranging from the gene to the ecosystem.

Plant Species Diversity

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 Gramineae excluding bamboos). The Pampa region in Argentina represents some of the highest diversity grassland, with more than 400 species of grasses (Cabrera, 1970). In North America, more than 250 native species are found in Tallgrass Prairie (Freeman, 1998), the vast majority of which are perennial grasses.

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 position 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 endemisms, however, the climatic and soil gradients within them have led to substantial 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 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 (Paruelo et al., 1998). 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).

Animal Species Diversity

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 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 a 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 is 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 vs. 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 diversity, 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 Prairie and Shortgrass Steppe (Lauenroth and Milchunas, 1992).

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 biodiversity 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 to 1000 times as great as vertebrate biomass (Groombridge and Jenkins, 2002). 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 (Ransom et al., 1998) and the nematode biomass was exceeded only by that of bacterial and fungal groups.

Soil Microbial Diversity

Microorganisms are broadly defined as a group of microscopic life forms that include bacteria, archaea, viruses and unicellular eukaryotes like some fungi and protists. The diversity of microorganisms is known in much less detail than that of plants and animals but it constitutes a very important component of the soil biota (van der Heijden et al., 2008). The large biomass of roots and other underground organs in grasslands and the high concentration of organic matter provide substrate for a large variety of microorganisms. The number of prokaryotes (bacteria and archaea) in grassland soils is estimated to be 32×10^{27} cells (Whitman et al., 1998). Soil microbes represent a very diverse group of organisms in grasslands soils with a variety of functional roles. For the Shortgrass Steppe, the relative importance in terms of biomass of the different functional groups is bacteria > fungi > nematodes > protozoa > macroarthropods > microarthropods (Lauenroth and Milchunas, 1992).

There is a tight association between soil microbial communities and plant species composition (Wardle et al., 2004). For example, arbuscular mycorrizal (AM) fungi are obligate root symbionts that are present in most terrestrial ecosystems and have roles in plant mineral nutrition, carbon cycling, and biotic interactions. The number of AM fungal taxa per host plant species is high in grasslands (8.3 fungal taxa per plant species) only higher in tropical forests (18.2 fungal taxa per plant species) (Opik et al., 2006). Also, AM fungal communities greatly differed in their composition in grassland ecosystems. In addition, bacteria and fungi communities differed in soils associated with plant functional types in grasslands. In the Great Plains of North America, the bacterial community that occurred under the mesquite shrub harbored greater levels of richness than those occurring beneath a C_3 perennial grass, a C_4 midgrass or a C_4 shortgrass communities (Hollister et al., 2010).

Biodiversity and Ecosystem Functioning in Grasslands

The relationship between biological diversity and the functioning of ecosystems has been central in ecology and grassland ecosystems have been crucial in testing those ideas. The biodiversity and ecosystem functioning hypothesis indicates that the rate of ecosystem processes, such as primary productivity or nutrient cycling, might increase linearly as species richness increases and that this relationship eventually saturates as ecological niches overlap increases (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 results can be interpreted as resulting from the sampling effect, which results from the increased probability of including species that outperform the others as the number of species in the mix increases (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 grows 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 Relative Yield Total (RYT) compares the performance of a mixture of species with the average of monocultures and indicates the strength of the biodiversity effect (de Wit and van den Bergh, 1965). Values

greater than 1 indicate that biodiversity is responsible for the increase in primary production.

The first large-scale field experiment was located in the North American Tallgrass Prairie and showed a saturating curve with 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 Europe and USA basically showed similar results (i.e., Hector *et al.*, 1999; Reich *et al.*, 2004; Roscher *et al.*, 2005). Grassland biodiversity–ecosystem-functioning studies yielded an average RYT of 1.2 with a range between 0.9 and 2.2 (**Figure 3**) (Flombaum and Sala, 2008). The only experiment performed in a natural ecosystem had an RYT significantly higher than all the rest of the experiments that were done using synthetic communities. This result reaffirms the role of biodiversity on ecosystem functioning in grasslands and suggests that the effect of biodiversity on ecosystem functioning might be even larger than previously thought. Consequently, expected global biodiversity loss (*see* The Future of Biodiversity in Grasslands) will have a large negative effect on grasslands primary production and carbon sequestration. It is likely that the magnitude of the biodiversity effect would be positively related to the co-evolutionary history of species in the mix and negatively to the frequency and intensity of disturbance (Sala, 2001), both characteristics would argue for a larger biodiversity effect in natural than in synthetic communities. The effect of the loss of biodiversity in grasslands and its effects on the C cycle would be an example of the synergism of global change drivers where biodiversity loss would constrain grassland ability to cope with the effect of other stressors such as climate change and ozone pollution.
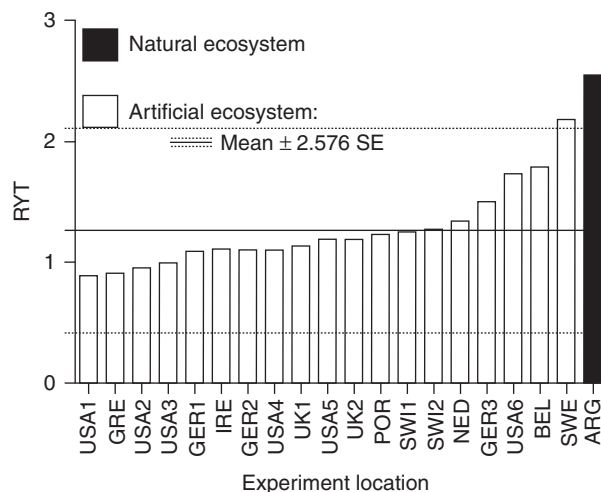
A large effort has been made in identifying the relative contribution of niche complementarity and sampling effect. Using analytical tools, Loreau and Hector (2001) found that niche complementarity was the most important mechanism to account for increases in primary production with biodiversity. Long-term field experiments in grasslands further strengthened this argument by showing that the niche complementarity increased while sampling effect decreased (Fargione *et al.*, 2007; van Ruijven and Berendse, 2009). After more than a decade of the first experiments performed in grasslands, a general consensus exists that plant diversity has a linear and positive relationship with net primary production, and that relationship is mostly due to niche complementarity (Hillebrand and Matthiessen, 2009; Hooper *et al.*, 2005).

The Future of Biodiversity in Grasslands

Biodiversity in grassland ecosystems is seriously threatened by human activity. Two independent studies that developed global scenarios of biodiversity change 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, grasslands may lose between 8% and 10% of the vascular plant species by the year 2050 (**Figure 4** and Sala *et al.*, 2005). Differences between these estimates are driven by different socio-economic scenarios with Order from Strength being the most pessimistic from the biodiversity point of view with 10% loss and Adapting Mosaic the most optimistic with 8% loss. Order from Strength is a scenario driven by security and protection issues that yield a fragmented world with islands of wealth isolated from the rest of the world where population growth and food demand remain highest (**Figure 4a**). High demand for food and low technology transfer from developed to developing nations result in large conversions of grasslands into croplands with the corresponding loss in biodiversity. In contrast, Adapting Mosaic is one of the most optimistic scenarios from the point of view of biodiversity loss where regional watershed-scale ecosystems are the focus of political and economic activity (**Figure 4b**). Local institutions are strengthened and societies develop a strong proactive approach to the management of ecosystems. Perhaps, the most striking feature of these scenario results is the small difference between the most optimistic and the most pessimistic scenarios. Even under the most optimistic scenario, large biodiversity losses are going to occur in grassland ecosystems.

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
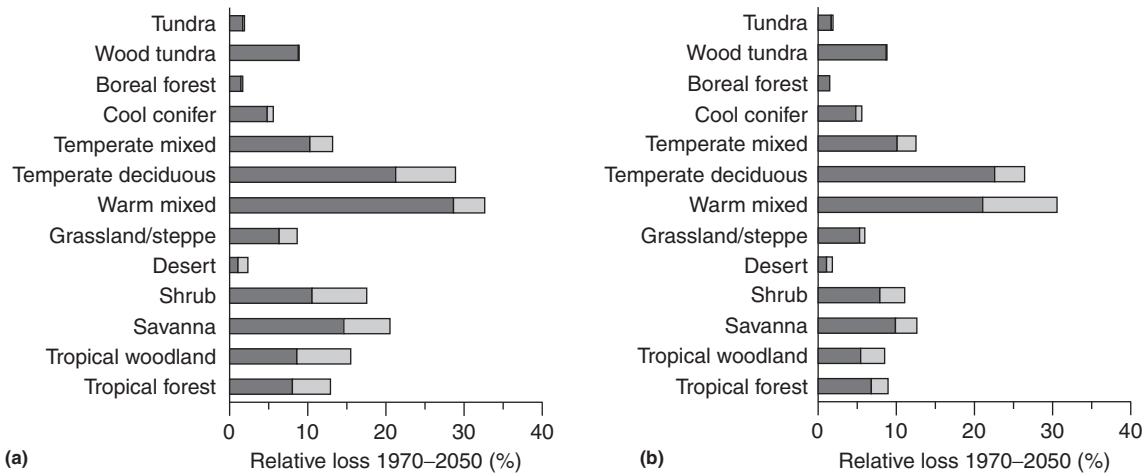

Figure 3   The effect of biodiversity on primary production in natural and artificial ecosystems. The RYT compares the performance of a mixture of species with the average of monocultures. Values greater than 1 indicate that biodiversity is responsible for the increase in primary production. The effect of biodiversity in natural ecosystem is larger than expected using artificial ecosystems Reproduced from Flombaum P and Sala OE (2008) Higher effect of plant species diversity on productivity in natural than artificial ecosystems. *Proceedings of the National Academy of Sciences of the USA* 105: 6087–6090.

Figure 4 Scenarios of biodiversity change for different biomes for the years 2020 and 2050. Bars represent relative losses of biodiversity of vascular plants through habitat loss for different biomes for two scenarios: (a) Order from Strength and (b) Adapting Mosaic. Losses of biodiversity would occur when populations reach equilibrium with habitat available in 2050 and are relative to 1970 values. Darker bars represent scenarios for 2020 and lighter bars for 2050. Adapted from original Figure 10.6 in Sala OE, van Vuuren D, Pereira H, *et al.* (2005) Biodiversity across scenarios. In: Carpenter SR, Pingali PL, Bennett EM, and Zure kM (eds.) *Ecosystems and Human Well-Being: Scenarios*, pp. 375–408. Washington, DC: Island Press.

most dramatic changes in land use in grasslands are those that result from conversion into croplands. The conversion into agricultural land is not expected to be even across the world but driven by patterns of food demand and population growth that indeed are quite idiosyncratic. For example, the IMAGE2 model (Alcamo, 1994) predicts for the year 2100 a large increase in agricultural area in Africa and a reduction in North America resulting from both an increase in demand and an increase in intensification respectively. 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.

The major driver of biodiversity loss in grasslands in the next 50–100 years will be land-use change followed by climate change (Sala *et al.*, 2000, 2005). The third driver of biodiversity change in grasslands will be nitrogen deposition. Densely human-populated regions where nitrogen deposition is the highest are predominantly located in temperate regions where the potential native vegetation is that of grasslands.

See also: Agricultural Invasions. Asia, Ecosystems of. Biodiversity and Ecosystem Services. Climate Change and Extinctions. Climate, Effects of. Desert Ecosystems. Ecosystems of South America. Endangered Ecosystems. Fires, Ecological Effects of. Grazing, Effects of. Herbaceous Vegetation, Species Richness in. International Organizations and Biodiversity. Loss of Biodiversity, Overview. Soil Biota, Soil Systems, and Processes. Terrestrial Ecosystems

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