

Biodiversity in Grasslands. Current Changes and Future Scenarios

Martín R. Aguiar¹

ABSTRACT

Loss of biodiversity is a pressing problem for the biosphere. Current estimations for one of the attributes of biodiversity – species richness – indicate that extinction rates are higher than in the recent past and are still increasing. The environmental drivers of species extinction rates are also changing other structural and functional attributes of biodiversity. The main causes of biodiversity loss are global; land use and land cover change has been proposed as having the biggest impact. The grassland biome, which includes a wide range of ecosystem types, from humid prairies to arid shrub–grass steppes, has been subjected to particularly intense pressure for the production of food and fibres, so current extinction rates of grassland species are expected to remain high or even increase. The main aim of this chapter is to consider current processes and future scenarios for grassland biodiversity. As one considers the future, it is useful to address three questions regarding biodiversity loss. First, what are the effects of the main drivers of biodiversity loss, and what are the main trends in the biodiversity of grasslands? Second, how will biodiversity continue to change after extinctions take place? Third, how can we manage grassland biodiversity in the transition to the new scenario? Currently, there is a lot more information available to answer the first question than there is information to address the other two. Nevertheless, it is necessary to address the second and third questions in order to develop proactive strategies for managing the transition to new scenarios.

¹IFEVA and Cátedra de Ecología, Facultad de Agronomía, Universidad de Buenos Aires. Av. San Martín 4453, Buenos Aires (1417). Argentina

INTRODUCTION

On the verge of the sixth major extinction event in the geological history of the Earth (Myers and Knoll, 2001), this chapter reviews both current and probable near-future trends in grassland biodiversity. Concern about biodiversity derives from two certainties. First, that changes in major drivers of ecosystem structure and functioning are global and affect all biomes. Second, that these changes will affect humanity through the erosion of the life-support systems of the Earth. In other words, there will be a reduction in ecosystem capability to provide natural resources and to process wastes (i.e. ecosystem services). Grasslands have been and still are central to the production of food and fibres for human use (Redman, 1999).

The main land uses in grasslands—agronomy and animal husbandry—involve four main activities:

- extraction of resources (e.g. mineral nutrients);
- changes in energy and material transfers (e.g. individual plant growth and nutrient mineralization);
- changes in species composition (e.g. addition of crops and weeds) and substances (i.e. agrochemicals, principally pesticides and fertilizers); and
- changes in the disturbance regime (e.g. cultivation, grazing).

These activities introduce major changes in the structure and functioning of ecosystems (see, for example, Aguiar *et al.*, 1996). However, superimposed on land use changes, grasslands are experiencing changes in other drivers, such as climate, atmospheric composition, and non-planned species exchanges, and these changes combine to threaten ecosystem integrity on a global scale (Vitousek *et al.*, 1997a).

Biodiversity has been identified as one of the best descriptors of ecosystem condition. Biodiversity is the sum of total biotic variation, from gene to landscape, but researchers have primarily focused on species diversity (Huston, 1994). This has resulted in the use of biodiversity and species richness as synonyms and a consequent need to relate species richness with ecosystem functioning (Chapin *et al.*, 2000). Over the past decades, ecologists have studied the determinants of species diversity (e.g. Hutchinson, 1959; MacArthur and Wilson, 1967; Tilman and Pacala, 1993; Huston, 1994; Hubbell, 2001) and the connection with ecosystem functioning (Chapin *et al.*, 2000). The issues are far from completely resolved, since many processes at different temporal and spatial scales contribute to or reduce species diversity and change ecosystem functioning (Huston, 1994; Lawton, 1995; Stohlgren *et al.*, 1999). Nevertheless, our current understanding confirms that human appropriation of Earth's ecosystems promotes the extinction of species at higher rates (Lawton, 1995; Rosenzweig, 1995) than in the past, in addition to extensive changes in ecosystem functioning (Vitousek *et al.*, 1997a).

Management for biodiversity conservation requires the integration of social and ecological systems into regional systems (cf. Chapin and Whiteman, 1998). Management of regional systems requires understanding of the main interactions between social systems and ecosystems. Scientists working in biophysical and social science, land managers, stakeholders and decision-makers should reach a common understanding in order to address the major causes of biodiversity loss, and to plan for the future use of natural resources. An integrated view of the social-ecological system is one of the main components of the new generation of projects studying biocomplexity. Biocomplexity theory deals with the study of complex systems and proposes complementing the study of parts of systems with the study of systems as a whole.

This chapter summarizes the main scenarios foreseen for the coming decades concerning the changes in biodiversity in grasslands. Written for grassland managers, the chapter starts by introducing a framework for discussing biodiversity. This framework allows the reader to escape from the usual trap of confounding biodiversity with species richness. Subsequently it addresses the question: “What are the scenarios of grassland biodiversity over the next few decades?” To answer this, the main drivers of changes in biodiversity and their impact on biodiversity are analysed. The chapter then addresses the question: “What will happen after extinction occurs?” In particular, “What types of species will dominate landscapes?” and “What will be the main pattern of evolution for the remaining species?” In the final section, the emerging concept of biocomplexity is discussed, and the main challenges that grassland ecologists will face during the next decades are proposed.

BIODIVERSITY AS A HIERARCHY

Biodiversity is, in some way, a fuzzy term, one that includes the sum of all biotic variation at three levels: intraspecific genetic variation; species diversity; and ecosystem diversity (Purvis and Hector, 2000). Being such a multidimensional system attribute, biodiversity cannot be reduced to a single number, such as species richness, so there is the need for a series of indicators that allows us to identify and measure the different attributes of biodiversity. Noss (1990) proposed a hierarchical framework to study the attributes of biodiversity. He proposed three complementary sets of attributes of biodiversity: compositional; structural; and functional (Table 11.1). The compositional attributes refer to the identity and variety of the elements included in the target system. They range from intraspecific genetic diversity (i.e. alleles), to landscape types (i.e. proportion of habitats). The structural attributes refer to the physical organization of the elements. They range from genetic structure (i.e. effective population size) to landscape structure (i.e. patchiness and connectivity among patches). The functional attributes include the ecological and evolutionary processes that organize ecosystems. They include gene flow, matter and energy exchanges, and disturbance regimes at the landscape level. In summary, biodiversity is a hierarchical concept that can be evaluated based on three complementary sets of attributes. Each set of attributes includes a variety of indices that can be measured.

Table 11.1 Biodiversity set of attributes according to Noss (1990). The three sets of attributes can be studied at four levels, from landscapes to genes. Levels are nested in a hierarchy and attributes are related by their effects on each other.

Biodiversity sets of attributes		
Compositional	Structural	Functional
Landscape types	Landscape patterns	Landscape processes (disturbance regime, land use trends)
Communities	Habitat structure	Interspecific interactions, ecosystem processes
Species, populations	Population structure (size distribution, sex ratio, spatial)	Demographic processes
Genes	Genetic structure	Genetic processes

Why is the Noss framework relevant to biodiversity assessment and monitoring in grasslands? There are two issues worth considering. First, the framework helps us to move away from using just a single attribute, such as composition, and a single indicator: diversity or richness. Considering the structural and functional attributes of biodiversity helps us to include essential aspects for understanding and monitoring ecosystem functioning. For example, at the population level, an important indicator of the population structure is spatial organization of genotypes. Spatial organization also affects other indicators, such as interspecific interactions (e.g. competition or facilitation) among plant populations. Another benefit of this framework is that it promotes the use of hierarchy theory. In other words, it promotes consideration of the levels above and below a target level of inquiry, from temporal and spatial perspectives. For example, fully understanding the effect of grazing on an individual species depends not only on knowledge of the interactions of that species with other species in the plant community (i.e. a functional attribute above the species level), but also awareness of the variability of ecotype diversity (i.e. a compositional attribute in the hierarchy below the species level).

GLOBAL CHANGE AND BIODIVERSITY SCENARIOS IN GRASSLANDS

Grasslands, in common with other major biomes, are experiencing the effects of major global changes. There are various possible scenarios of change in biodiversity for the next century, according to the report by Sala *et al.* (2000). The report discusses the sensitivity of biomes to the different global changes. They screened five drivers of change: land use; climate; nitrogen deposition; biotic exchanges; and atmospheric CO₂. A projected scenario of biodiversity results from multiplying the relative importance of the change in the drivers, by the impact on biodiversity of those changes.

Grasslands show intermediate effects from most of the drivers, except for land use. Changing land use will have a major impact on biodiversity, since it reduces habitat availability. Climate changes are expected to have less impact on grasslands – which are located mostly at temperate and intermediate latitudes – compared with higher latitude biomes, such as tundra (Walter, 1984). Nitrogen deposition will certainly have a major impact in N-limited systems. In general, grasslands are not the most N-limited biome, so the impact of this driver was assumed to be intermediate. Biotic introductions are also intermediate, because while mild habitat conditions facilitate establishment of invaders, existing levels of species diversity constrain resource availability. Finally, atmospheric changes in CO₂ will have a relatively high impact on grasslands because of the frequent mixed composition in terms of C₃ and C₄ species. In general, however, it is considered that these drivers have only an intermediate impact on biodiversity.

Since none of these drivers acts alone, the report proposes that it is possible to consider three types of interaction: additive; response to only the driver with the maximum effect; and multiplicative. After considering these interactions, grasslands were ranked in the upper half of the biomes studied, in terms of altered biodiversity. This means that grasslands are ecosystems where some of the largest changes in biodiversity are expected to take place. Other systems, such as Mediterranean scrub or savannahs, usually linked to grasslands under the category of “rangelands”, ranked close to grasslands when the additive or the multiplicative model of interaction among drivers was assumed. The following use Noss’ framework, presented in the previous section, to discuss the consequences of changes in the drivers that Sala *et al.* (2000) identified as those most important for grassland biodiversity, namely land use, climate, nitrogen deposition, biotic exchanges and atmospheric CO₂.

LAND USE EFFECTS ON BIODIVERSITY

Grassland “land use” includes all human activities involving grasslands. These activities range from grazing and management of domestic animals, to land conversion to crops, forest or urbanization. This section discusses the effect on biodiversity of grazing and land conversion to crops and forests. Since grazing and cropping in grasslands have been extensively discussed elsewhere, the objective is to focus on Noss’ framework in order to organize and review the information that already has been presented. The objective is therefore twofold. First, to review the ways in which land use affects grassland biodiversity, and, second, to use the hierarchical and multiperspective model proposed by Noss.

Grazing by domestic herbivores

Domestic herbivores are selective grazers and promote changes in plant community composition (i.e. the composition attributes of biodiversity). This was soon noted by rangeland ecologists. Dykterhuis (1949) proposed a theory of rangeland management based on this knowledge. According to this theory, by changing stocking rates it was possible to manage plant community composition. This statement proved, however, not to be valid for all conditions and ecosystems. New knowledge enriched the model of rangeland management. For example, it is widely accepted that transition from one community composition to another may not be linear. In other words, changes in plant community composition may not be gradual, but triggered as disturbance reaches a certain threshold. The currently accepted model of grazing effects on plant dynamics indicates that a given ecosystem includes several states (i.e. different species compositions). The transition from one state to another is not solely the result of stocking rates. For example, variability between years in climate and in disturbance regime also play major roles in determining the occurrence of change (Westoby, Walker and Noy-Meir, 1989).

In addition to community composition, other attributes of biodiversity change as a result of grazing. In arid and semi-arid ecosystems, vegetation is frequently organized in a dual-phase mosaic composed of patches with high vegetation cover (or plant density) dispersed in a matrix of low plant cover (Figure 11.1) (Aguiar and Sala, 1999). This horizontal organization of plant canopy was reported in an early study (Noy-Meir, 1981), but its origin is not fully comprehended. A growing number of studies enrich our knowledge of the processes that maintain this particular community pattern. More importantly, ecologists are using the concept of a dual-phase mosaic to create and build communities with a particular structure (Boeken and Shachak, 1994) (Figure 11.1, left). This structural dimension in plant community biodiversity is gaining recognition as an issue needing consideration.

Many ecosystem and population processes are influenced by the spatial organization of the vegetation mosaic (Aguiar and Sala, 1999). For example, in banded vegetation in Mexico and Australia, water availability and hydrological balance are controlled by the vegetation pattern (Figure 11.1, centre). The matrix functions as a source area that transfers water to the vegetation patches, allowing greater primary production, or a particular flora (Cornet, Dehlhume and Montaña, 1988; Montaña, López and Mauchamp, 1990; Gutiérrez *et al.* 1993; Ludwig and Tongway 1995). The effects of grazing on spatial structure are not clear. Since grazing generates a pattern in vegetation (Sala, 1988), the effect of grazing depends on the vegetation pattern being analysed (banded or spotted mosaic) (Aguiar and Sala, 1999). In some cases, such as in the banded vegetation in Australia, it has been suggested that overgrazing disrupts the mosaic (Ludwig and Tongway,

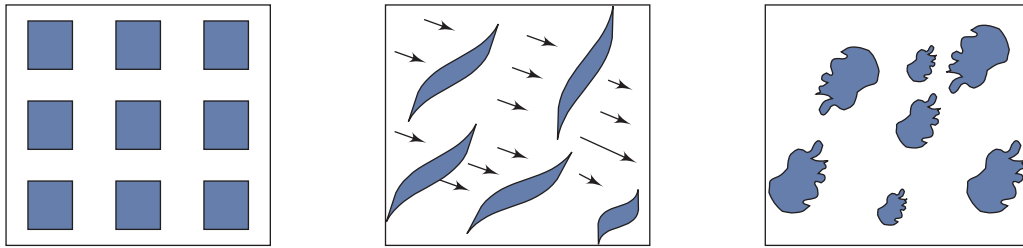


Figure 11.1 Structural biodiversity in vegetation mosaics at the landscape and community levels.

On the left is a schematic example of a vegetation mosaic with a regular pattern in agro-ecosystems.

The centre image is a banded pattern, such as those described in semi-arid landscapes with a gradual slope, found in Australia, Africa or North America. Arrows indicate the direction of water flow in the inter-band areas. Water infiltrates in the bands.

The mosaic on the right is a patch pattern as described in semi-arid ecosystems of South and North America.

1995). A recent review of the effects of grazing on spatial structure of plant communities found that currently there is no strong evidence that grazing disrupts vegetation patterns (Adler, Raff and Lauenroth, 2001). In summary, a spatially-explicit view of community and ecosystems allows new perspectives for processes (i.e. dispersal, population dynamics, and plant–plant and plant–animal interactions) and functions (i.e. soil organic matter dynamics, and water and nutrient circulation). Whereas structural diversity has been recognized at the landscape level, structural diversity has been ignored at the community level, even though long proposed (Watt, 1947).

From the compositional perspective, grazing has a major impact not only on species composition (as already discussed), but also at the population level. Population genetic diversity and structure of preferred species can change as grazing drives plant density down (Schemske *et al.*, 1994). Rangeland theory assumes that, with proper management, species reduced by overgrazing can recover if the physical environment has not changed drastically. In other words, there are no demographic constraints to recovery for the few remaining plants. From the genetic point of view, however, the situation may be different. As the size of a population decreases, genetic variability is reduced. Genetic drift, the loss of genetic diversity that occurs in small size populations, contributes to the process (Schemske *et al.*, 1994). Grazing can exert strong selection pressure, promoting traits that increase tolerance or avoidance of herbivory. In small populations, genetic drift is a common process, and erodes genetic variability in a random fashion, without increase in fitness. Low genetic diversity levels may therefore constrain population sustainability by reducing the capacity of the population to cope with environmental variability. Essentially, adequate management can promote an increase in population numbers, but not necessarily an increase in genetic variability, and therefore the limited genetic diversity of the recovering population can restrain population viability.

Most reviews of biodiversity mention genetic diversity as one of the most pressing problems associated with human-induced global changes. However, for grasslands, there is not enough information on this factor. More information is needed in order to understand the relationship between grazing and genetic variability. More information is needed on the structural and functional attributes of genetic diversity. In other words, it is necessary not only to know how much variability exists in a population, but also how it is spatially distributed (i.e. structural attributes of genetic diversity). Also, it is necessary to address the genetic processes, such as migration of genes. As plant density decreases, distances between individuals increase. Two

processes maintain the unity of this fragmented population: movement of gametes (i.e. pollen) and seed dispersal. All the information must be spatially explicit since grazing is heterogeneous in space at different scales (Senft *et al.*, 1987).

In summary, since the emergence of new theories for range management (Westoby, Walker and Noy-Meir, 1989), most efforts have been aimed at evaluating changes in species abundance and diversity, and at estimating the effect of these changes on ecosystem processes, such as primary production and decomposition (Milchunas and Lauenroth, 1993). These changes increase along productivity gradients from arid to subhumid grasslands. The next efforts to understand the effects of grazing on grasslands need to be oriented towards understanding of the structural attributes of biodiversity, from population to community. There is evidence that the spatial structure of populations and communities control many processes (Cornet, Dehlloume and Montaña, 1988; Montaña, López and Mauchamp, 1990). Gathering spatially explicit data will promote our understanding of the effect of a spatially heterogeneous process such as grazing. Currently, there is information on the three sets of attributes of biodiversity at regional and landscape scales (Turner, Gardner and O'Neill, 2001).

Replacement of grassland by other land cover types

Grassland biodiversity is negatively affected by two sources of land cover change: cropping and forestry. These activities differ in their impacts on ecosystem structure and function. Cropping changes above- and below-ground plant biomass in a sudden fashion, but it also promotes large changes in soil organic matter (Burke, Elliott and Cole, 1995). In contrast, forestry changes land cover more slowly, from a grass-dominated to a tree-dominated system. A forest-dominated system changes the light environment, but can also change soil nutrient dynamics (Ong *et al.*, 1991).

Cropping has affected the three sets of biodiversity attributes (Table 11.1). For example, in the Rolling Pampa of Argentina, one of the most productive grasslands in temperate South America, the structural and compositional attributes of the region have changed because of land-cover changes. The original grassland during the nineteenth century was turned into a mosaic of crops, cultivated pastures and semi-natural grasslands (Viglizzo *et al.*, 2001). The total cultivated area at the start of the twentieth century was 6 million hectares, but by 1984 it had increased to 26 million hectares (FAO, cited in Ghersa and León, 1999). The spatial structure of the mosaic changes the inherent patterns of the landscape, which in turn changes the attributes of biodiversity.

Land use regimes in the pampas changed the compositional attributes of biodiversity according to the particular management application at the paddock level. Therefore diversity of the landscape changed as new crops (e.g. soybean) or management (e.g. no-tillage cropping) were added, or with changes in the relative area devoted to different crops in the mosaic (Hall *et al.*, 1992). Associated with the change in the structure of the vegetation mosaic, several community processes (functional attributes) changed as well. For example, many species became locally extinct, while others colonized and invaded the landscape. The original number of plant species in well-drained soils has been estimated to have been around 222; in 1999, in maize crops, the number of species had decreased to 99 (Ghersa and León, 1999). Of the 99 species, only 54 species had been present in the original grassland, the remaining 45 species were exotic. At the same time that such changes in community composition and processes occur, other ecosystem processes change too. For example, agricultural practices foster changes in decomposition rates, exportation of nutrients, soil structure degradation and erosion, and seasonality in production (Bernardos *et al.*, 2001). Noss (1990) proposed the inclusion of all these processes as functional attributes of biodiversity.

As new or old species increase in abundance in the different areas of the agricultural mosaic, new interactions develop within the biotic community. For example, in the pampas agro-ecosystems there has been an increase in species that produce secondary products such as terpenoids, thyophenes and alkaloids. It is suggested that this increase is associated with soil degradation that promotes stress-tolerant species in particular locations within the mosaic. Further changes in the rates of processes may develop from change in community composition. For example, pest outbreaks may be negatively affected since, from the perspective of the pest, the landscape has become fragmented and diverse from a structural point of view (Ghersa and León, 1999).

As cropping fragments a landscape, other human activities generate different impacts on species population dynamics. Fences, roads, railways and rights of way under telephone and electricity transmission lines are not cropped. These areas develop semi-natural vegetation and form a network of corridors that facilitates organism dispersal throughout the region. In this sense, analyses of the effects of land use require the assessment of the spatial structure of the landscape and the interactions of species with the landscape mosaic. In perspective, data from the pampas agricultural mosaic indicate that land use will lead to more changes than just a reduction in the number of species. Indeed, the structural attributes of biodiversity change dramatically in grasslands that are transformed to crop production. At the same time, the functional attributes of biodiversity will also change. Furthermore, these changes occur not only at the scale of individual fields or paddocks but also at the landscape and regional scale.

Conversion to forest has been the other major land cover change experienced by grasslands. This change occurs directly as a result of land management decisions or as an indirect effect of other decisions. Many countries, such as Argentina, are promoting forestation as a way to ensure meeting requirements for cellulose fibres. In general, forestations are monospecific. Many of these forestations are financed by credit from international agencies. In the case of Argentina, the World Bank has financed a forestation plan that has been successful in capturing the attention of landowners. From 1992 to 1999, the surface area converted to forest in the pampas grassland was 46 870 ha (SAGPYA, 1999). Forestation clearly changes the structural attributes of biodiversity.

Unplanned conversion of grassland to forest has been described in many ecosystems distributed throughout the Americas, Australia and Africa (Briggs, Hoch and Johnson, 2002). Rates of change are high. Data from the tallgrass prairie in North America indicate that 40 years are enough to develop a closed canopy forest once there are some focal plants established. Many processes contribute to tree invasion and establishment in a grassland ecosystem. Seed availability is affected by changes in dispersal corridors. Seedling establishment and survivorship is influenced by changes in the disturbance regime. In the pampas, the human-developed network of corridors host up to 40 woody species, mostly trees (Ghersa *et al.*, 2002). Either wind or animals, including domestic herbivores, and birds disperse the successful tree invaders (Mazia *et al.*, 2001). At the same time, changes in disturbance regime might be the principal cause of successful establishment and growth of seedlings. Briggs, Hoch and Johnson (2002) pointed out that grazers reduce fuel load and reduce fire frequency, promoting *Juniperus virginiana* success in the tallgrass prairie. Data from the pampas indicate that there are species-specific traits that promote success of trees in grasslands. For example, in the pampas, competition from tussock grasses was intense enough to preclude establishment of two out of four tree species tested (Mazia *et al.*, 2001).

Effects of both planned and unplanned forestation on the functional attributes of grassland biodiversity are similar. Both biodiversity and herbaceous productivity decrease. Briggs, Hoch and Johnson (2002) report a decrease in richness (10 m² plots) from around 30 species to less than five species. At the same time, invasion susceptibility of the new forest community also changes.

Mazia *et al.* (2001) indicate that under forest canopies none of the seedlings survived of the four tree species tested. In other words, this indicates that forests were less susceptible to invasion than grasslands. Herbaceous biomass decreased from 384 g/m² in annually burned grassland to 0.2 g/m² underneath the *Juniperus* forest. In the long term, forestation promotes other changes as well. In the pampas, mineral soils in 50-year-old forests had lower pH (4.6 to 5.6), 40 percent lower exchangeable Ca, and three times the Na level compared with soils in neighbouring grasslands (Jobbagy and Jackson, 2003). Data indicate that these changes result from recycling and redistribution of elements rather than from leaching facilitated by organic acids produced by trees.

NITROGEN INPUTS AND ATMOSPHERIC CO₂ INCREASES

N and atmospheric CO₂, two limiting plant resources, are globally increasing as a consequence of human activities and are therefore treated together here. Nitrogen inputs in ecosystems over approximately the last 50 years have been roughly double natural N inputs (Vitousek *et al.*, 1997b). This widespread change has been particularly intense in agricultural lands, mostly located in grassland regions. Fertilization changes the functional attributes of biodiversity, changes the rate of processes of such denitrification or leaching, and changes rates of extinction and colonization in plant communities. Management of nitrogen cycling includes the addition of fertilizers, land rotations that include nitrogen-fixing crops, and tillage to increase mobilization of N stored in soil organic matter. N fertilizer use in croplands has increased constantly since 1940 (Vitousek *et al.*, 1997b). Increments in N input occurred first in the developed countries, and subsequently in developing countries. Most of the information on the effects of N addition refers to changes in community composition and ecosystem functioning.

Nitrogen addition experiments in grasslands indicated that one of the consequences is a reduction in plant diversity. For example, the Rothamsted Park Grass Experiment, one of the longest and oldest experiments, indicates that N addition promotes the dominance of a few species and the suppression of many other species (Silvertown, 1980). Species loss was five times greater in the treatment with the highest N addition, compared with no N addition. Similar results were found in North American grasslands (Tilman, 1987). In Europe, agriculture fertilization and N deposition on heathland communities have promoted a replacement of the original shrub community with one dominated by grass species (Aerts and Berendse, 1988).

In general, N addition increases the dominance of fast-growing species with high shoot–root ratio (Tilman and Lehman, 2001). This trait enables those species to successfully compete for light, which is usually limiting in productive habitats. This contrasts with the natural situation in grasslands, where dominant species usually exhibit traits suitable to dealing with soil limitations (Lauenroth and Coffin, 1992). Additionally, use of N fertilization promotes acidification of soil.

Atmospheric CO₂ enrichment is also expected to effect grassland composition and functioning (Paruelo, 2002). The importance of CO₂ enrichment derives from its effects on plant carbon gain and water status. Absorption of CO₂ through stomata is associated with plant water losses. Water use efficiency (i.e. grams of CO₂ absorbed per gram of water lost), increases as CO₂ increases (Paruelo, 2002). Early predictions of the impact of CO₂ enrichment on grasslands indicated that plant community composition would change. Essentially, it was proposed that C₃ grass species would outcompete C₄ grasses. However, a meta-analysis of experimental data indicated that C₃ and C₄ species responded similarly to CO₂ enrichment (Wand, Midgley and Jones, 1999). C₃ species increased total biomass by 44 percent and C₄ by 33 percent.

Results from a Mediterranean annual grassland showed that the dominant grass (*Avena barabata*) increased seed production and plant survival, resulting in an overall increase in plant density (Jackson *et al.*, 1994). These changes occurred not only because of higher CO₂ concentration, but changes were also found in soil water dynamics associated with higher water use efficiency. Plant transpiration was less under elevated CO₂ than under ambient concentrations. Lower transpiration at the beginning of the growing season also increased soil water content.

In temperate grasslands in Canada, Potvin and Vasseur (1997) compared community dynamics of ambient and CO₂-enriched plots. After three years, they found that ambient plots had lower species richness and more dominance than enriched plots. In enriched plots, early successional species (*Plantago major*) responded to CO₂, reducing the increase in later successional species (*Agropyron repens*). In general, these authors found that dicotyledenous species advanced while grasses retreated. Their results parallel responses measured in a tallgrass prairie in central North America and in a Swiss pasture (Potvin and Vasseur, 1997). In contrast, Paruelo (2002) refers to a study in a tallgrass prairie that found no changes in the C₃-C₄ balance after eight years of enrichment. Other disturbances, such as fire and grazing, had a greater effect on species composition.

In synthesis, increments in N and CO₂ availability might promote changes both in the compositional attributes of biodiversity (genotypes in a population or species in a community) and in the functional attributes of biodiversity (transpiration, carbon gain). In essence, change in the compositional attributes parallels change in the functional attributes of biodiversity.

BIOTIC EXCHANGE

Biotic exchange among ecosystems has been profoundly affected by human activities worldwide (Mooney and Hobbs, 2000). Human activities facilitate both species migration and community invasiveness. Species migration can increase by exchanges of species, both accidentally and deliberate. Community susceptibility to invasion can increase because of changes in the disturbance regime or in other environmental drivers. In the case of temperate grasslands, species invasions have been particularly conspicuous (Chaneton *et al.*, 2002).

Biotic exchange greatly increases genotypic and species homogenization at various levels from patches to regions. Species extirpation and invasions increase the abundance of a few, very successful invaders. Rusch and Oesterheld (1997) found that grazing promoted the introduction of many exotic dicotyledenous forb species, increasing species diversity. Species invading grassland ecosystems include various functional groups of plants. For example, in the pampas in South America, Chaneton *et al.* (2002) found that most of the cool and warm season invasive species were forbs. In North American grasslands, the invasion by the annual grass *Bromus tectorum* is one of best case studies (Mack, 1981). Invasion of *Bromus* took place at the end of the nineteenth century in the Great Basin region, displacing both shrubs and perennial grasses. Plant cover reduction by heavy grazing prompted and facilitated invasion. Dry biomass of *Bromus tectorum* increased fire frequency, promoting the disappearance of perennial and dominant grasses and shrubs. The site became dominated by annual grasses and shrubs (*Gutierrezia sarothrae* and *Chrysothamnus* spp.) (West, 1979). *Bromus tectorum* competes with established perennial grasses for water, but the critical element in its success is the increased fire frequency: from every 80 years to every 4 years (Melgoza, Nowak and Tausch, 1990). Perennial grasses went locally extinct, as they could not cope with the new fire regime. D'Antonio and Vitousek (1992) reviewed information on the ecosystem effects of biological invasion by exotic grasses and found that this

pattern of invasion and change of fire regime seems to be common. According to them, biological invasions have caused more species extinction than climate change or atmospheric composition change. They stress the fact that biological invasions change not only the community diversity (compositional attributes of biodiversity) but also the functioning of ecosystems (functional attributes of biodiversity). Other ecosystems processes such as energy fluxes and material cycles are also affected by invasions.

AFTER EXTINCTION

Previous sections analysed scenarios for different attributes of biodiversity. They also presented examples in which changes in the drivers promoted changes in the various attributes of biodiversity. This section abandons the use of the three sets of attributes of biodiversity proposed by Noss and focuses on species diversity alone. It moves on one step and assumes that diversity reduction has effectively occurred. According to current estimations, the extinction rate is higher than in the recent past, and it is increasing. What will occur after extinction? Will extinction alter the evolutionary processes by which diversity is generated? Will any particular types of species dominate future ecosystems? Will biodiversity eventually recover? What will be the recovery rates? These are relevant questions, if we hope to develop proactive management strategies for the “new world.” Sponsored by the National Academy of Science of the United States of America, a colloquium discussed these issues (*The Future of Evolution* [contributed papers can be downloaded free from the *Proceedings of the National Academy of Science* Internet site]). Experts in different fields evaluated the information recovered from, for example, the geological record. They also evaluated current knowledge on species requirements and species strategies in relation to environmental templates in new ecosystems. The direction of evolution is not predictable, but knowing what happened in the past may indicate how evolution might proceed (Myers and Knoll, 2001).

Various patterns of evolution might occur after extinctions, since major disruptions are taking place in very diverse biomes, such as tropical forests, grasslands, wetlands, coral reefs and estuaries. Several ideas summarize the current view of the future (Myers and Knoll, 2001). As extinction proceeds, an outburst of speciation may occur because of a large number of vacant niches and the fragmentation of populations. A few ecological types may possibly account for most of the speciation because of the predominance of human-dominated ecosystems throughout the biosphere. For example, it is possible that opportunistic and generalist species may proliferate. Disruption in particular ecosystems, such as tropical forests, may affect evolutionary patterns in other ecosystems. It has been proposed that tropical forests are the engines for new species, and their disappearance may hamper future evolution in neighbouring grasslands. As we evaluate future evolution, it is necessary to consider not only environmental changes but also biotic changes. For example, extinction will affect the “biodisparity” within the biota. In other words, extinction can preferentially affect species with particular morphology and physiology. In this sense, future patterns of evolution will develop from an incomplete biota. Because of anthropogenic effects it is probable that higher taxa and guilds are candidates for extinction, and for this reason, re-diversification might be limited.

Recovery rates (i.e. the velocity of rebuilding species diversity) after extinction are difficult to estimate from the geological record. These records are also not completely appropriate for this endeavour. Perturbations that caused extinction events were probably intense, but short-lived. In contrast, we are currently facing global changes that may alter the biosphere and the major drivers of extinction over longer time periods. Jablonski (2001) indicates that recovery would be

slow in terms of a human time scale. However, many aspects of recovery, such as the spatial context (e.g. source–sink dynamics) and the reorganization of ecosystems after extinction, increase the complexity and decrease the predictability of the recovery process. More geographical analyses of the fossil record may shed light on the issue. Erwin (2001) found no clear relationship between the magnitude of extinction and the rate of recovery. Theoretical modelling confirmed that empty niches should refill with new species rapidly, but empirical studies showed complex dynamics. Erwin submits that, since extinction may disrupt ecosystem structure and function, it is necessary to accept that recovery will involve the concurrent redevelopment of species diversity and ecosystem processes. In this sense, some studies reveal a time lag in recovery, as well as the reappearance of groups that disappeared again subsequently in the recovery process.

Other evidence indicates that rates of diversification after extinction may not be slow. Cowling and Pressey (2001) present the case of the Cape Floristic Region in South Africa, where species diversification occurred rapidly after climate change in the late Pliocene. During that time, the climate became Mediterranean, and fires became frequent. In the Cape Floristic Region, diversification did not occur randomly among ecological groups. Cowling and Pressey (2001) indicate that, for example, species from the woody groups are “low [stature], fire killed (i.e. non-sprouting) shrubs with poorly dispersed seeds, small and short-lived seed banks, and insect-pollinated flowers.” According to them, all these characteristics lead to rapid generation turnover, which promotes diversification. A short-lived seed bank favours non-overlapping generations and promotes the expression of novel characteristics in each generation. Fire induces population fragmentation and local population extinction, and short dispersal distances induce isolation and diversification of populations in different habitats.

Tilman and Lehman (2001) discuss the particular case of plant species extinction and the subsequent diversification in the grasslands biome. They use a set of well-established theoretical ideas to address two issues. First, what will be the expected changes in the factors that constrain plant population growth, and what will be the consequences of the predicted changes? Second, assuming a certain type of new environment, what will be the probable types or guilds of plant species evolving from the remaining guilds? Plants respond to major constraints by adjusting allocation of resources to roots, stems, leaves and seeds (recruitment of new individuals). Most grasslands or woody–grass ecosystems are strongly constrained by soil resources (e.g. nitrogen, water). The plant types adapted to these constraints allocate an important amount of growth to roots. The consequence is that these species guilds are poor competitors for light, or poor recruiters or dispersers, or a combination. As discussed above, two of the major environmental changes are an increase in nitrogen availability and environmental fragmentation. In grasslands, most species are not suited to successfully compete in this new environment. They either lack the ability to compete for light or lack dispersal capacity to overcome human-created barriers or fragmentation. Few species will succeed in this environment. These species are usually classified as weedy because of their ability to respond rapidly to resource availability, their poor competitive ability, and their good dispersal ability (Tilman and Lehman, 2001).

To address the second issue, Tilman and Lehman (2001) use a simple model that considers a trade-off between competitive ability and dispersal ability. They assume that after extinction a single type of a plant species remains. This type, as already discussed, is a good disperser but a poor competitor. Their model projects that, after enough generations, two types of species will dominate: one will be a very poor competitor but a good disperser, whereas the other will be a good competitor, but a poor disperser. After a very long time (0.5 million years) the model predicts the evolution of more than 20 species types, scattered along a competition-dispersal gradient.

The model does not consider other factors that can alter these results, such as periodic invasions of species that can displace the species evolving *in situ*. As was reviewed above, biotic exchange would be a predominant process in the future. There is evidence that, in the past, invasive species altered the evolution pathway of native species (Mooney and Cleland, 2001). Alteration of evolution derives from many possible processes, including competitive exclusion, niche displacement, hybridization, introgression, predation and extinction itself. It is also necessary to say that invaders contribute to biodiversity and also evolve in response to the physical and biotic environment.

It is clear that estimating post-extinction patterns and rates of evolution of species diversity (compositional attribute of biodiversity) is a hard task and our predictive capabilities are still poor. Trying to include in the picture the other attributes of biodiversity (i.e. structural and functional) is a remaining task. A complementary strategy would be to monitor changes in the three attribute sets as a way to gain an understanding of the entire process. As several participants in the colloquium agreed, a proactive response to the extinction process is necessary (Cowling and Pressey, 2001; Novacek and Cleland, 2001; Woodruff, 2001; Ehrlich, 2001; Bazzaz, 2001). Monitoring and adaptive management are complementary tasks. Adaptive management is not an easy task due to the many issues at stake (social, economic, cultural and technical), and also due to our currently poor forecasting power (Clark *et al.*, 2001) and because of the science-policy gap (Bradshaw and Borchers, 2000). These topics will be discussed in the next section.

MANAGEMENT OF BIOCOMPLEXITY—THE NEXT FRONTIER

Human pressure on the biosphere will increase because of both population growth and increasing per capita consumption. This pressure will not only be intense but also widespread in grasslands, as crop and animal husbandry occurs mostly in this biome. As discussed above, any project oriented to managing the biodiversity transition must include, among other drivers of global change, human-driven land-use change as a major component of the scenario (Meyer and Turner, 1992). Since the social system affects and is affected by ecosystem structure and functioning, there is increasing interest in studying the interactions between social and natural systems (Redman, 1999; Chapin and Whiteman, 1998; Bradshaw and Bekoff, 2001).

Social systems and ecological systems have interacted at least since the beginning of human existence. In this sense, the study of ancient human impact on ecosystems could be used as the prologue to the design of sound management strategies. Redman (1999) integrates archaeological and historical records in a model of the interactions between natural and social systems. He identifies three different phases in human systems: expansion, intensification and abandonment. In this conceptual model, human society is initially constrained by factors from the social system and the natural systems. Humans promote changes in land use and land cover, acting on landscape organization and biological and biogeochemical processes. As a consequence, human society is released from the constraints and initiates a phase of human expansion. Paralleling changes in the natural system, the human system also becomes more complex as new social groups develop (e.g. administrators, religious organizations and military). More resources are needed to support the expansion and the new functions in the society. There is also the need to accumulate reserves to meet society needs in bad years. All these changes result in intensification of natural resource exploitation. Pressures on ecosystems move them to a structure and function beyond their resilience, leading to the next phase: collapse and abandonment. One important feature of this model is that the social group that makes the decisions about natural resource management is not the same group that is involved in working the land, i.e. decision-makers have no direct contact with natural resources.

Based on the present review, grasslands, as socio-ecological systems, should be observed from three different perspectives: biophysical, productive-technical, and socio-economic (Figure 11.2).

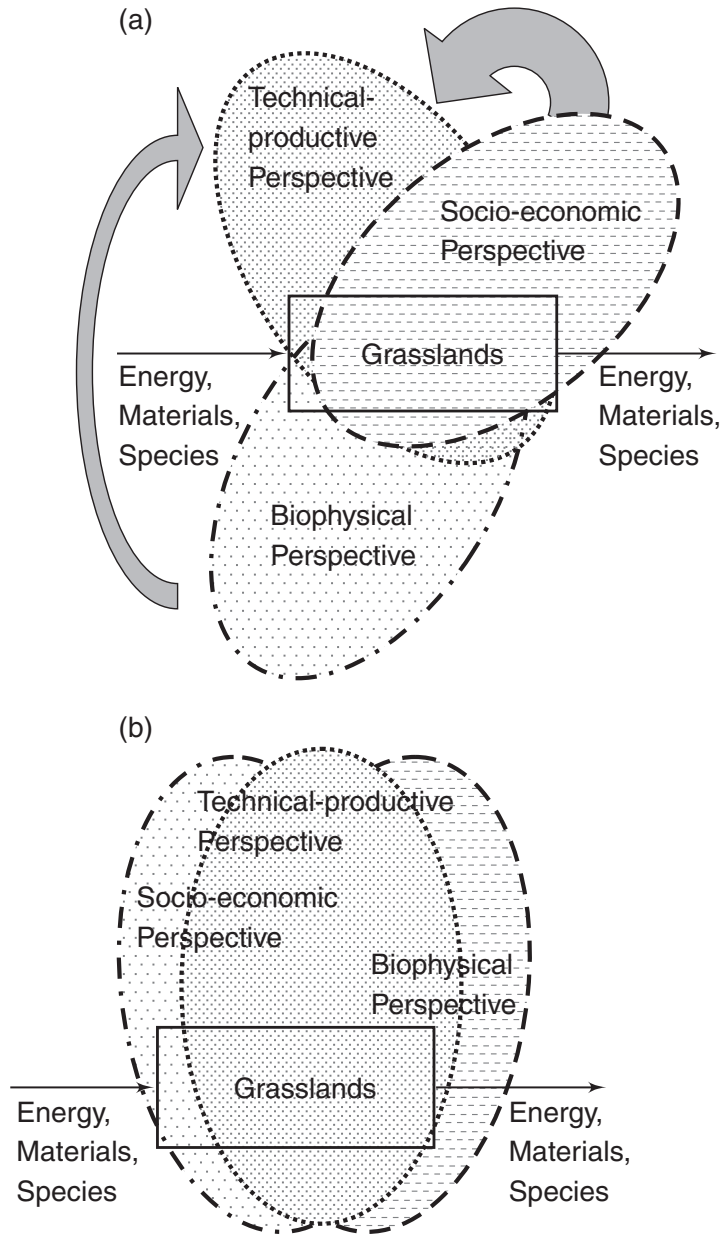


Figure 11.2 Schematic representation of the three perspectives from which grasslands can be analysed.

- (a) Currently the biophysical perspective has little influence on the technical-productive and socio-economic perspectives, being the least important determinant of the way that grasslands are utilized.
- (b) Represents a complementary evaluation of grassland management.

The biophysical perspective is the one with which most ecologists are familiar. Biodiversity is studied to understand its relationship with the physical and biotic environment. The productive-technical perspective refers to all the management, technology and tools developed to modify grassland structure and function. It includes, for example, the selection of species genotypes, control of natural flora or fauna, and modification of soil conditions through tillage, fertilization or irrigation. The socio-economic perspective includes the social, political, economic, cultural and religious or spiritual aspects of grasslands. These three perspectives should be complementary, although not always true in practice. The biophysical perspective, in theory, may influence the productive-technical perspective, since the biological and physical components constrain what can be done and achieved. In practice, productive-technical decisions are mostly associated with the socio-economic perspective. For example, commercial strategy is a rather large determinant in management decisions. On many occasions, it goes against what the biophysical perspective indicates (sometimes even against what the technical-productive perspective indicates). For example, the development of a new herbicide is an effective weed control, but in time (i.e. several generations of the weed species or several cultivation cycles) the weed community changes its composition, or the weed population develops resistance, thus reducing the herbicide's value for crop production. Delaying the appearance of herbicide resistance includes the cost associated with incomplete or imperfect weed control, but it results in a long-term benefit. Incomplete weed control permits survival of susceptible genotypes and delays the dominance of resistance in the weed population. Another example, at a global scale, is the failure to fully implement the Kyoto protocol on CO₂ emissions. Here, policy decisions may hamper efforts to adjust technical-productive procedures that reflect the biophysical perspective (Durand, 2002).

Conserving and managing biodiversity both need the integration of all three perspectives in a complementary way (Figure 11.2b). This is not an easy task and requires a new framework, rooted in the understanding that a collaboration of social and biophysical sciences is necessary (Bradshaw and Bekoff, 2001). That framework also needs to incorporate the idea that socio-ecological systems are complex systems (Anonymous, 1999). A new area of interest is the study of biocomplexity. According to the US National Science Foundation,

“biocomplexity refers to phenomena that arise as a result of dynamic interactions that occur within biological systems, including humans, and between these systems and the physical environment. From individual cells to ecosystems, these systems exhibit properties that depend not only on the individual actions of their components, but also on the interactions among these components and between these components and the environment.”

The complexity of these systems derives not necessarily from them having many components. On the contrary, the main reason is that their behaviour cannot be predicted from the knowledge of their parts and feedback among the system components (Zimmer, 1999). Complexity derives from different system properties, such as variability in their components, context-dependent processes, non-linear processes, time-delay responses, and chaotic behaviour. Both social and ecological systems have these characteristics. For example, communities and populations are composed of different species and genotypes, respectively. Usually, biological responses have short time lags, if we consider morphological, physiological or behavioural responses. However, time lags become long if we consider numerical responses, such as birth and mortality rates. Also, many population and ecosystem processes are non-linear.

The study of socio-ecological systems requires a new approach that includes not only the study of the parts but also the study of the whole. It also requires a major collaborative effort of social and biophysical sciences. Complexity theory can bridge the gap between sciences, since both

social and biophysical systems are complex (Anonymous, 1999; Bradshaw and Bekoff, 2001). It also requires that biophysical sciences are considered as part of society and therefore objects of study themselves.

Another issue that hampers the integration of the three perspectives of grasslands systems is that the power of prediction of biophysical models decreases as spatial and temporal scales increase from the local paddock to the global, and from days to decades, respectively. Uncertainty in forecasts is at the root of the science-policy gap. Uncertainty and complexity are part of the normal lives of scientists, whereas “society and policy-makers seek certainty and deterministic solutions” (Bradshaw and Borchers, 2000). In this scenario of uncertainty, it is difficult to apply a standard decision-making process in social-ecological systems (Walker *et al.*, 2002). An alternative approach is a resilience analysis and management that seeks to define a desirable configuration of systems that reinforces system resilience, which is the capacity to cope with future shocks. Resilience results from three characteristics: the amount of change that the system can undergo without altering its configuration; the capability of self-organization; and the capacity to learn and adapt. In this framework, system stakeholders are key players in identifying both threats to the system and management practices that maintain and promote resilience. Their experiences are used to define thresholds in system attributes (i.e. desirable structure and functions, such as debt–income ratio). For example, perception of the desertification process by stakeholders may be very vague, but income reduction is readily perceived. Connecting with some key features of an ecosystem, e.g. woodiness or presence of weed seeds in wool, may be easier than comprehending any indicator of biodiversity, such as the ones presented here. Participation of stakeholders in the analysis fosters a change in perception of uncertainty from ignorance to knowledge. This is a key change in order to reduce the science-policy gap.

CONCLUSIONS

Future scenarios of biodiversity indicate that grasslands, as with other biomes, will suffer from biodiversity loss or erosion. The main causes of biodiversity losses are global changes; however, land use (a regional-scale phenomenon) might have the biggest impact. As we move into this new scenario with diminished biodiversity, it is useful to address three aspects of the biodiversity erosion. First, “What are the main trends in the biodiversity of grasslands, and what are the effects of the main drivers of biodiversity loss?” Second, “What are the changes expected in the biodiversity of grasslands after extinctions have occurred.” Third, “How can we manage the biodiversity of grasslands in the transition to the new scenario?”

Biodiversity includes many levels of organization, and many temporal and spatial scales. It is a useful and necessary concept to address the main characteristics of ecosystems. In time, this concept has become vague, as scientists commonly use “biodiversity” as a synonym for species richness. Noss (1990) proposed a framework that allows us to monitor and manage biodiversity. This framework for biodiversity has three sets of attributes: compositional, structural and functional. Adopting this three-attribute-set framework allows us to address the many changes that are occurring at different spatio-temporal scales and in biological hierarchies. It also ensures that we include the spatial structure of ecological systems in our analyses. Our current understanding points to the fact that spatial structure is a key determinant of many processes, across populations, communities and ecosystems. Many examples show that land cover and land use changes are eroding all sets of attributes, not just the compositional.

It is necessary to begin to understand the future patterns of evolution and change of ecological systems as many species disappear, landscapes become fragmented, communities are invaded, and nutrient cycles are modified. A simulation exercise, based on the compositional attributes alone, allows a first approximating of the evolutionary paths. In the case of plants, it seems that weedy species will predominate. However, in time it is possible that new species will evolve from this group.

Since grasslands will continue to be heavily used ecosystems, it is necessary to implement new, sound management practices to address biodiversity. Humankind is a component of eco-social systems, and therefore management needs to be based on a complementary use of biophysical, technical and socio-economic perspectives. In order to address a complementary view of grasslands, more interactions between social and ecological scientists are necessary. Complex system theory, and the biocomplexity framework in particular, provides a template for studying these interactions. Accepting that uncertainty is a key attribute of both social and ecological systems is the next frontier in studies of biocomplexity and biodiversity.

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REFERENCES

- Adler, P., Raff, D. & Lauenroth, W.K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*, **128**: 465–479.
- Aerts, R. & Berendse, F. 1988. The effect of increased nutrient availability on vegetation dynamics in wet heathlands. *Vegetatio*, **76**: 63–69.
- Aguiar, M.R., Paruelo, J.M., Sala, O.E. & Lauenroth, W.K. 1996. Ecosystem responses to changes in plant functional types: An example from the Patagonian steppe. *Journal of Vegetation Science*, **b**: 381–390.
- Aguiar, M.R. & Sala, O.E. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology and Evolution*, **14**: 273–277.
- Anonymous. 1999. Complex systems. *Science*, **284**: 79–109.
- Bazzaz, F. 2001. Plant biology in the future. *Proceedings of the National Academy of Science (USA)*, **98**: 5441–5405.
- Bernardos, J.N., Viglizzo, E.F., Jouvett, V., Lértora, F.A., Pordomino, S.J. & Cid, F.D. 2001. The use of EPIC model to study the agroecological change during 93 years of farming transformation in the Argentine pampas. *Agricultural Systems*, **69**: 215–234.
- Boeken, B. & Shachak, M. 1994. Desert plant communities in human made patches – implications for management. *Ecological Applications*, **4**: 702–716.
- Bradshaw, G.M. & Borchers, J. 2000. Narrowing the science-policy gap: Uncertainty as information. *Conservation Ecology*, **4**. (see <http://www.cosecol.org/vol4/iss1/art7>).
- Bradshaw, G. M. & Bekoff, M. 2001. Ecology and social responsibility: the re-embodiment of science. *Trends in Ecology and Evolution*, **16**: 460–465.
- Briggs, J.M., Hoch, G. & Johnson, L. 2002. Assessing the rate, mechanisms, and consequences of the conversion of Tallgrass Prairie to *Juniperus virginiana* forest. *Ecosystems*, **5**: 578–586.
- Burke, I.C., Elliott, E. & Cole, C.V. 1995. Influence of microclimate, landscape position, and management on soil organic matter in agroecosystems. *Ecological Applications*, **5**: 124–131.
- Chaneton, E., Perelman, S., Omacini, M. & León, R. 2002. Grazing, environmental heterogeneity, and alien plant invasions in temperate Pampa grasslands. *Biological Invasions*, **4**: 24–24.

- Chapin, F.S. & Whiteman, G. 1998. Sustainable development of the boreal forest: interaction of ecological, social, and business feedbacks. *Conservation Ecology [online]*, 2(2): 12. (see <http://www.consecol.org/vol2/iss2/art12>).
- Chapin III, F.S., Zaveleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Lavorel, S., Reynolds, H.L., Hooper, D.U., Sala, O.E., Hobbie, S.E., Mack, M.C. & Díaz, S. 2000. Consequences of changing biotic diversity. *Nature*, 405: 234–242.
- Clark, J.S., Carpenter, S.R., Barber, M., Collins, S., Dobson, A., Foley, J., Lodge, D., Pascual, M., Pielke, R., Pizer, W., Pringle, C., Reid, W.V., Rose, K.A., Sala, O.E., Schlesinger, W., Wall, D.H. & Wear, D. 2001. Ecological forecasts: an emerging imperative. *Science*, 293: 657–660.
- Cornet, A., Dehhoume, J. & Montaña, C. 1988. Dynamics of striped vegetation patterns and water balance in the Chihuahuan Desert. pp. 221–231, in: H. During, M. Werger and J. Willens (eds). *Diversity and pattern in plant communities*. The Hague: SPB Academic Publishing.
- Cowling, R. & Pressey, R. 2001. Rapid diversification: Planning for an evolutionary future. *Proceedings of the National Academy of Science (USA)*, 98: 5452–5457.
- D'Antonio, C. and Vitousek, P. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, 23: 63–87.
- Durand, F. 2002. Ceguera ante una amenaza mortal. [Blindness against a mortal threat]. *Le Monde diplomatique*, 42: 28–29.
- Dykterhuis, E.J. 1949. Condition and management of range land based on quantitative ecology. *Journal of Range Management*, 2: 104–115.
- Ehrlich, P. 2001. Intervening in evolution: Ethics and actions. *Proceedings of the National Academy of Science (USA)*, 98: 5477–5480.
- Erwin, D. 2001. Lessons from the past: Biotic recoveries from mass extinctions. *Proceedings of the National Academy of Science (USA)*, 98: 5399–5402.
- Ghersa, C.M. & León, R.J.C. 1999. Successional changes in agro-ecosystems of the rolling pampa. pp. 487–502, in: L.R. Walker (ed). *Ecosystems of disturbed ground*. (Ecosystems of the World, vol. 16). Amsterdam, The Netherlands: Elsevier.
- Ghersa, C.M., de la Fuente, E., Suárez, S. & León, R.J.C. 2002. Woody species invasion in the Rolling Pampa grasslands, Argentina. *Agriculture, Ecosystems and Environment*, 88: 271–278.
- Gutiérrez, J., Meserve, P., Contreras, L., Vasquez, H. & Jaksic, F. 1993. Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porleria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia*, 95: 347–352.
- Hall, A.J., Rebella, C.M., Ghersa, C.M. & Culot, P.H. 1992. Crop systems of the pampas. pp. 413–449, in: C.J. Pearson (ed). *Field crop ecosystems*. (Ecosystems of the World, vol. 18.) Amsterdam, The Netherlands: Elsevier.
- Huston, M. 1994. *Biological diversity: The coexistence of species on changing landscapes*. Cambridge UK: Cambridge University Press. 681p.
- Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton, NJ: Princeton University Press. 375p.
- Hutchinson, G. 1959. Homage to Santa Rosalia; or, why are there so many kinds of animals. *American Naturalist*, 93: 145–159.
- Jablonski, D. 2001. Lessons from the past: Evolutionary impacts of mass extinction. *Proceedings of the National Academy of Science (USA)*, 98: 5393–5398.
- Jackson, R.B., Sala, O.E., Field, C.S. & Mooney, H.A. 1994. CO₂ alters water use, carbon gain, and yield for the dominant species in a natural grassland. *Oecologia*, 98: 257–262.
- Jobbagy, E. & Jackson, R. 2003. Patterns and mechanism in soil acidification in the conversion of grasslands to forest. *Biogeochemistry*, 54: 205–229.
- Lauenroth, W.K. & Coffin, D.P. 1992. Belowground processes and the recovery of semiarid grasslands from disturbance. In: M.K. Wali (ed). *Ecosystem Rehabilitation*, Vol. 2. The Hague: SPB Academic Publishing.
- Lawton, J.H. 1995. Population dynamic principles. pp. 147–163, in: J.H. Lawton and R.M. May (eds). *Extinction rates*. Oxford, UK: Oxford University Press.
- Ludwig, J. & Tongway, D. 1995. Spatial organization of landscape and its function in semiarid woodland, Australia. *Landscape Ecology*, 10: 51–63.
- MacArthur, R. & Wilson, E. 1967. *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Mack, R. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agroecosystems*, 7: 145–165.
- Mazia, C.N., Chaneton, E.J., Ghersa, C.M. & León, R.J.C. 2001. Limits to tree species invasion in pampean grassland and forest plant communities. *Oecologia*, 128: 594–602.
- Melgoza, G., Nowak, R.S., & Tausch, R.J. 1990. Soil water exploitation after fire: Competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia*, 83: 7–13.

- Meyer, W. & Turner, B.L. 1992. Human population growth and global land-use/cover change. *Annual Review of Ecology and Systematics*, **23**: 39–61.
- Milchunas, D.G. & Lauenroth, W.K. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**: 327–366.
- Montaña, C., López, J. & Mauchamp, S. 1990. The response of two woody species to the condition created by a shifting ecotone in an arid ecosystem. *Journal of Ecology*, **78**: 789–798.
- Mooney, H. & Hobbs, R. (eds). 2000. *Invasive species in a changing world*. Washington, DC: Island Press.
- Mooney, H. & Cleland, E. 2001. The evolutionary impact invasive species. *Proceedings of the National Academy of Science (USA)*, **98**: 5446–5451.
- Myers, N. & Knoll, A. 2001. The biotic crisis and the future of evolution. *Proceedings of the National Academy of Science (USA)*, **98**: 5389–5392.
- Noss, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, **4**: 355–364.
- Novacek, M. & Cleland, E. 2001. The current biodiversity extinction event: Scenarios for mitigation and recovery. *Proceedings of the National Academy of Science (USA)*, **98**: 5366–5470.
- Noy-Meir, I. 1981. Spatial effects in modeling of arid ecosystems. pp. 411–432, in: D. Goodall and R. Perry (eds). *Arid ecosystems: Structure, functioning, and management*. Vol. 2. Cambridge, UK: Cambridge University Press.
- Ong, C.K., Corlet, J.E., Singh, R.P. & Black, C.R. 1991. Above- and-below ground interactions in agroforestry systems. *Forest Ecology and Management*, **45**: 45–56.
- Paruelo, J.M. 2002. Temperate grasslands. In: J. Canadel and H. Mooney (eds). *The earth system: Biological and ecological dimensions of global environmental change*. (Encyclopaedia of Global Environmental Change, Vol. 2). New York, NY: John Wiley.
- Potvin, C. & Vasseur, L. 1997. Long-term CO₂ enrichment of a pasture community: species richness, dominance, and succession. *Ecology*, **78**: 666–677.
- Purvis, A. & Hector, A. 2000. Getting the measure of biodiversity. *Nature*, **405**: 212–219.
- Redman, C. 1999. *Human impact on ancient environments*. Tucson AZ: University of Arizona Press. 239p.
- Rosenzweig, M. 1995. *Species diversity in space and time*. Cambridge, UK: Cambridge University Press.
- Rusch, G. & Oesterheld, M. 1997. Relationship between productivity, and species and functional group diversity in grazed and non-grazed pampas grasslands. *Oikos*, **78**: 519–526.
- SAGPYA [Secretaría de Agricultura, Ganadería, Pesca y Alimentación]. 1999. Ocho años de implementación de plantaciones forestales (RPPF) [Eight years of implementation of the forestry promotion programme]. *SAGPYA Forestal*, **13**: 11–13.
- Sala, O.E. 1988. The effect of herbivory on vegetation structure. pp. 317–330, in: M.J.A. Werger, P.J.M. van der Aart, H.J. During and J.T.A. Verhoeven (eds). *Plant form and vegetation structure*. The Hague: SPB Academic Publishing.
- Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Hueneke, L.F., Jackson, R., Kinzig, A., Leemans, R., Lodge, D., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes M.T., Walker, B.H., Walker, M. & Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science*, **287**: 1770–1776.
- Schemske, D., Husband, B., Ruckelshaus, M., Goodwille, C., Parker, I. & Bishop, J. 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology*, **75**: 584–606.
- Senft, R.L., Coughenour, M.B., Bailey, D., Rittenhouse, L., Sala, O. & Swift, D. 1987. Large herbivore foraging and ecological hierarchies. *BioScience*, **37**: 789–799.
- Silvertown, J. 1980. The dynamics of a grassland ecosystem: botanical equilibrium in the Park Grass Experiment. *Journal of Applied Ecology*, **17**: 491–504.
- Stohlgren, T.J., Binkley, D., Chong, G., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, **69**: 25–46.
- Tilman, D. 1987. Secondary succession and pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, **57**: 1898–214.
- Tilman, D. & Pacala, S. 1993. The maintenance of species richness in plant communities. pp. 13–25, in: R. Ricklefs and D. Schluter (eds). *Species diversity in ecological communities*. Chicago IL: University of Chicago Press.
- Tilman, D. & Lehman, C. 2001. Human-caused environmental change: impacts on plant diversity and evolution. *Proceedings of the National Academy of Sciences (USA)*, **98**: 5433–5440.
- Turner, M., Gardner, R. & O'Neill, R. 2001. *Landscape ecology in theory and practice*. New York NY: Springer Verlag.
- Viglizzo, E.F., Lértora, F.A., Pordomino, S.J., Bernardos, J.N., Roberto, Z.E. & Del Valle, H. 2001. Ecological lessons and applications from one century of low external-input farming in the pampas of Argentina. *Agriculture, Ecosystems and Environment*, **83**: 65–81.
- Vitousek, P., Mooney, H., Lubchenko, J. & Melillo, J.M. 1997a. Human domination of Earth's ecosystems. *Science*, **277**: 494–499.

- Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H. & Tilman, D. 1997b. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications*, 7: 737–750.
- Walker, B., Carpenter, S., Anderis, J., Abril, N., Cumming, G., Janssen, M., Lebel, L., Norberg, J., Oeterson, G. & Pritchard, R. 2002. Resilience management in social-ecological systems: a working hypothesis for participatory approach. *Conservation Ecology*, 6: 14. [online] (See: <http://www.concecol.org/vol6/iss1/art14>)
- Walter, H. 1984. *Vegetation of the Earth*. 3rd edition. Berlin: Springer Verlag.
- Wand, S., Midgley, G. & Jones, M. 1999. Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO₂ concentration: a Meta-analytic test of current theories and perspective. *Global Change Biology*, 5: 723–741.
- Watt, A. 1947. Pattern and process in plant community. *Journal of Ecology*, 35: 1–22.
- West, N.E. 1979. Basic synecological relationships of sagebrush-dominated lands in the Great Basin and the Colorado Plateau. pp. 33–41, in Anon. *The Sagebrush Ecosystem: A Symposium*. Utah State University, College of Natural Resources, Logan, Utah.
- Westoby, M., Walker, B. & Noy-Meir, I. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, 42: 266–274.
- Woodruff, D. 2001. Declines of biomes and biotas and the future of evolution. *Proceedings of the National Academy of Science (USA)*, 98: 5477–5480.
- Zimmer, C. 1999. Life after chaos. *Science*, 284: 83–86.