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Edited by Kjell Danell, Patrick Duncan, Roger Bergstrom and John Pastor

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Introduction

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Biodiversity and productivity vary strongly among ecosystems: understanding the causes of these variations is a primary objective of ecology. To date a few overarching principles have been established. One is the species-area relationship: the species diversity of a system depends principally on its area, and some major mechanisms underlying this principle have been identified (Rosenzweig 1995). The structure and dynamics of plant communities also affect biodiversity profoundly. Edaphic conditions set the bounds for plant communities, and fire can be a key determinant of their structure and diversity. In addition, at least in some ecosystems, large herbivores are 'keystone' species, so the systems have very different structures according to whether large herbivores are present or absent. There is also some evidence that large herbivores affect plant productivity, from modelling (de Mazancourt *et al.* 1998) as well as empirical work (McNaughton 1985).

Understanding the role of large herbivores is therefore important for ecology, and also because the abundance of these animals can have profound effects on the conservation status of other species, through their impact on plant communities. However, the literature on these questions is rather difficult to access especially for people who are not academic ecologists. Reviewing the impact of large herbivores on ecosystems was identified as a priority in the Action Plan for the Large Herbivore Initiative for Europe and Central Asia (see <http://www.largeherbivore.org>). In some areas the ungulate populations are 'overabundant' and have serious negative impacts on forestry, agriculture and biodiversity. In other areas the

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ungulate populations are approaching extinction. There are thus many urgent management and conservation problems connected to large herbivores, and an accessible review of existing knowledge is urgently needed to underpin progress towards effective management.

In May 2002 Kjell Danell, Roger Bergström and John Pastor convened a workshop in Sweden to review 'The Impact of Large Mammalian Herbivores on Biodiversity, Ecosystem Structure and Function' and this book is the result of the work that started there. It focuses on wild large herbivores since information on domestic animals is voluminous and easier to access (though it could also benefit from being analysed to answer ecological questions!). Our main aim was to provide an up to date review of existing knowledge on the impact of large herbivores on species richness, ecosystem structure and function in the major habitats of the world. We also explore what is known about the consequences of global change on large herbivores populations, and their impact on ecosystems, and what needs to be done to improve our understanding of this crucial area.

The first chapter, '**Large herbivores across biomes**' by **H. Fritz and A. Loison**, presents the major communities of wild large herbivores in all the continents. For the purposes of this book, we define large herbivores as even-toed (Artiodactyla) and odd-toed ungulates (Perissodactyla) over 5kg, and elephants (Proboscidea). The abundance of large herbivores, at least in Africa at a regional scale, are determined ultimately by the abundance of their resources. The general principles underlying the diversity of their communities in all the continents are reviewed, starting with what is known about their palaeohistory. The patterns of distribution of some of the key life history traits are also reviewed, body size, mating system, sexual dimorphism and litter weight. The different body sizes are distributed across habitats and feeding guilds in log normal (hump-backed) distributions, whose modes increase with openness of the habitats, and this is true for marsupials as well as eutherians. Dimorphism in body mass is closely related to polygyny in Artiodactyla, but not in the other groups, so other variables are clearly important here. Demographic strategies, which also vary considerably, nonetheless show some clear patterns: large herbivores share high and relatively constant adult survival, relatively early and variable age at maturity, and a relatively low and very variable juvenile survival. These patterns appear to hold true across phylogeny, biomes, habitat and feeding types.

The following chapters in the first part of the book deal with determinants of the dynamics of large herbivore populations and communities,

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notably the linkage between resource abundance and population dynamics, the capacity of large herbivores to cope with seasonality in resources and in climatic conditions, and the interplay between large herbivores and large predators.

In Chapter 2, **'Living in a seasonal environment'** by J. Moen, R. Andersen and A.W. Illius, the focus is on a biome where seasonality is extreme, the Arctic. The effects of climatic variability on population sizes are analysed, and then the mechanisms are explored by evaluating the effects of environmental stochasticity on life history tactics of large herbivores (e.g. capital vs. income breeding), and the role of body size. Many models of global change predict an increase in the season of vegetative growth, which is already detectable, and the resulting increase in plant growth will generally be positive for large herbivores as both plant biomass and nutritional quality will increase. The decrease in snow cover (in some areas) will also be positive for large herbivores as they will have a longer period for body growth and an increased survival during the shorter winters. However, it is unclear what effect this will have on population dynamics: if climate change leads to increased animal growth and survival, the animal populations may enter winter at densities too high to be supported by winter resources. These climate changes may even result in lower accessibility of winter forage which could cause declines in calf body weight and survival during winter. Long-term monitoring is clearly essential, and coupled models of plant and animal dynamics like those of Illius and O'Connor (2000) could help to direct management of these systems, which are so sensitive to damage by overgrazing.

In Chapter 3, **'Linking functional responses and foraging behaviour to population dynamics'** by A.W. Illius, an in depth review is given of what is known about a key interface – the interaction between large herbivores and their food resources. Our knowledge of the underlying principles is reviewed, distinguishing the way consumption rates respond to food abundance (i.e. the functional response) from the way the size of the consumer population responds to variations in food consumption (the numerical response). The work of Spalinger and Hobbs (1992) provides a systematic means of analysing functional responses and evaluating biologically meaningful parameters. This is used to review the state of the art in foraging behaviour, diet selection and food intake of wild and domestic herbivores. Andrew Illius concludes by stating 'there are a priori and empirical grounds for the propositions that optimal patch use is not an appropriate model of resource use by browsing mammalian herbivores, and that longer-term diet optimization, i.e. the trade-off between diet

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quality and daily intake rate, is a more likely explanation of their foraging behaviour'.

Approaches to describing how consumer populations change in response to the average per capita food intake are then reviewed, from the simplistic/abstract representations of ecological interactions, such as Lotka-Volterra coupled differential equations to the mechanistic approach of Illius and Gordon (1999). An alternative approach has been developed by Owen-Smith (2002) who describes consumer-resource systems in terms of biomass dynamics, rather than numbers of consumers, and uses aggregated efficiencies of assimilation, metabolism, repair and senescence to model aggregated population dynamics.

In Chapter 4, **'Impacts of large herbivores on plant community structure and dynamics'** by A.J. Hester, M. Bergman, G.R. Iason and J. Moen, the focus is on the main direct impacts of herbivores on shrub and woodland systems to complement the later reviews, which cover more tree-dominated habitats. Their review covers the effects on individual plants (or ramets) and the range of responses of individual plants to herbivory, as a basis from which to explore the complexities of processes operating at the plant community level. Large herbivores make foraging decisions at a range of spatial (from bite to landscape) and temporal scales (from seconds to years), and plants also respond to herbivore impacts at a similar range of scale (plant part to community). This makes the identification of key processes affecting plant/herbivore interactions and the mechanisms driving plant community responses to herbivores quite a challenge. Some of the apparent controversies in the literature about herbivore influences on vegetation may be due to this difficulty.

Although most direct effects on plants, by grazing or browsing, are negative, indirect effects on seed dispersal, in the gut or on the body, are largely positive. Although some of the seeds do not survive herbivore digestive processes, others require passage through the gut of a herbivore for germination, or at least benefit from it. Further, the effects of large herbivores on seeding establishment are generally positive. Effects of large herbivore activities on plant growth and mortality can of course be strong; these are reviewed in relation to the type of tissue which is affected, the extent and frequency of off-take, and the herbivores involved.

Removal of plant parts above the ground inevitably affects below-ground processes as well. Reallocation of resources, at least in grasses, usually leads to increased shoot growth (i.e. to restoration of root:shoot ratios after damage). Above-ground herbivory can also induce changes in mycorrhizal fungi, thereby affecting nutrient uptake and subsequent

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growth and survival. Most studies show declines in mycorrhizal colonization as a result of herbivory, which can have powerful effects on the dynamics of the plant communities.

Plant responses to herbivores are reviewed, including defences (physical and chemical) and tolerance. Plants can avoid large herbivores through their spatial location, visibility (apparency), or by producing defence structures such as thorns, hairs or thick cuticles. They may also produce 'allelochemicals'; several hypotheses have been proposed to explain their ecological and evolutionary occurrence: the merits of these hypotheses, particularly the 'carbon-nutrient balance' hypothesis, are reviewed. The conditions determining 'tolerance' and 'compensation' are reviewed: although plants are most commonly detrimentally affected by herbivory, there is a long-running debate as there are examples of exact- or overcompensation in a considerable number of studies. Most of these, however, were short-term responses and might not accurately reflect long-term fitness – an important distinction.

There is a wealth of literature on the impact of large herbivores on plant diversity (species, structure and genetic), but still much controversy. This is probably due to both the complexity of the subject and a scarcity of long-term controlled studies where all main driving factors are understood. Most studies indicate that herbivores are more likely to increase the diversity and spatial heterogeneity of plant communities. However, the authors of this chapter show that there are exceptions, and that the conditions under which herbivores increase or decrease diversity and heterogeneity, and the mechanisms involved, are still not fully understood.

Chapter 5, '**Long-term effects of herbivory on plant diversity and functional types in arid ecosystems**' by **D. Ward**, addresses two contrasting yet widely held beliefs about the dynamics of the vegetation in arid ecosystems: first, that abiotic factors have more impact than biotic factors (principally because herbivores are limited at low densities by sparse resources), so herbivory by mammals is relatively unimportant in ecosystem functioning and biodiversity maintenance, and secondly that heavy grazing has caused land denudation and desertification in semi-arid regions such as the Sahel of Africa. It is important here to distinguish between short-term effects of herbivory (which lead to the removal of phytomass) and long-term ones (which lead to changes in productivity and the species composition of the plant communities). David Ward starts by showing that the results of long-term studies of the effects of large mammals on arid vegetation are not consistent. In some areas the impact

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is strong, in others weak. Ward argues that the inconsistency in the results of the long-term studies may result from oscillations of vegetation and herbivore populations: migratory or nomadic movements of the animals could lead to contrasting pressure of herbivory at times of the year, such as the growing season, that are crucial for the dynamics of the plants.

Some of the most interesting effects of herbivory on plant diversity result from the effects of selective herbivory on the relationships among plant functional types, in particular herbaceous vs. woody plants. Ward focuses on the phenomenon of 'bush encroachment', as evidence is accumulating that suggests this trend is a general one in arid and semi-arid savannas throughout the world. He illustrates it from arid regions ranging from the Namib and Kalahari deserts, to the Mitchell grass plains of Australia via the southern Sahara, the Negev and central Asian deserts, and reviews the general explanations that have been proposed for bush encroachment. The first is Walter's two-layer hypothesis, based on tree-grass competition. Later models propose that trees and grasses coexist in a state between that of grassland and forest because the plant communities are 'pushed back' into the savanna state by frequent disturbances (human impact, fire, herbivory and drought). Ward then describes the results of experiments to test some of these models, and shows that the results open new perspectives for understanding the fundamental processes and for management of bush encroachment. Under the conventional two-layer competition hypothesis, grazing during years with less than average precipitation should be reduced to a minimum so as not to give the trees a competitive advantage. By contrast, the new results suggest that bush encroachment may not occur when water is limited and consequently such a management protocol would be futile.

Grazing responses in arid and semi-arid rangelands in winter rainfall regions differ from those in summer rainfall regions, and plant height may be a more important factor than palatability, life history or taxonomic affiliation in determining responses to herbivory. Ward argues that the 'classical' theory of grassland response to grazing which defines plants as increasers or decreasers has some value in explaining plant responses, but should be replaced by a theory which considers plant size and other relevant traits such as palatability and specific leaf area. More studies on more continents are also needed to tease apart the effects of evolutionary history of grazing and abiotic environmental factors on grazing responses and plant functional traits.

Chapter 6, '**The influence of large herbivores on tree recruitment and forest dynamics**' by R. Gill, shows that the effects of large herbivores

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on tree regeneration can be grouped broadly into two main types. Firstly, the effects of feeding on seeds, seedlings and bark, which are damaging, and delay forest succession or accelerate senescence. Secondly, the effects which promote regeneration and thus tend to advance forest succession. There appear to be at least four mechanisms involved in this latter group: regeneration may be promoted through seed dispersal, protection from thorny plants, reduced competition, or, lastly, by reduced fire frequency or fire temperatures as a result of reduced fuel. In general, the retarding effects of herbivory appear to be more prevalent in woodlands and forests, whereas facilitation is more likely to occur in open habitats. The fact that these two contrasting processes occur in different communities has led to the suggestion that large herbivores cause a cycle of succession, where the serial stages of open ground, young trees, maturing woodlands and senescent stands finally give way to open ground again. Large herbivores can therefore create more dynamic woodlands, where changes in tree cover occur continually, and where light-demanding species are favoured at the expense of shade-tolerant ones.

There is evidence for the simultaneous existence of all stages of this cycle, and there is no reason to suggest that the rates of regeneration and senescence will be balanced. Rates of tree regeneration and damage by large herbivores can be highly variable. Facilitation by thorny plants will depend on the suitability of the site for the nurse species. Each species of herbivore has a unique pattern of habitat and diet selection. As a result, the impact of large herbivores can lead to dominance of either grassland or of closed-canopy woodland. The effect of large herbivores on nutrient flows can bring about enduring changes in vegetation composition. Since the amount of food for herbivores can be sharply reduced by shade, animal populations will decline if trees grow dense enough to form closed-canopy woodland over an extensive areas, which then limits the extent to which herbivores can maintain openings. In the savanna regions of Africa, switching between woodland and grassland states can occur: as a result of a combination of grazing, elephants and fire, woodlands in the Serengeti-Mara region were opened up in the 1960s, but began to recover again in part of the region during the 1980s, when elephant numbers were severely reduced. These changes suggest that savanna ecosystems may be unstable, or have alternative stable states, and events affecting herbivore numbers or grazing pressure can prompt major changes in vegetation structure.

Evidence from exclosures suggests that the selective browsing by deer tends to reduce tree species diversity. Unfortunately there is insufficient

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information to generalize for other herbivores in forest habitats, although a study of the impact of elephants found that diversity of trees and shrubs were reduced, but diversity of plants near ground level was increased. A similar result was reported for moose browsing, where diversity of the smallest trees increased, but apparently not in older trees.

In Chapter 7, '**Large herbivores: missing partners of western European light-demanding tree and shrub species?**' by F.W.M. Vera, E.S. Bakker and H. Olf, the consequences of the presence of large herbivores for the vegetation and other biota are addressed. A major criterion for the selection of sites for the conservation of nature in western Europe has always been 'naturalness'. Curiously there has been little effort to analyse what the natural landscapes looked like. It has often been claimed that temperate Europe without human influence would have been almost entirely covered with a closed canopy broad-leaved forest, the 'classical' forest theory. However, these forests contained indigenous species of large herbivores (aurochs, tarpan, red deer, moose, roe deer and European bison). These animals were assumed not to have had a substantial influence on the forest, but to follow the development in the vegetation. Vera *et al.* reviews knowledge from a wide range of disciplines, including palaeontology, palynology, evolutionary ecology, and history, and presents a provocative point of view of the role of large herbivores in temperate forests. They suggest that large herbivores were in fact very important influences on natural temperate forests, and created a park-like landscape over much of temperate Europe with bulk grazers like cattle and horse playing key roles in the processes involved.

These 'wood pastures' have an extremely high diversity of plant and animal species, because of the structural diversity of the vegetation. The oak has a special place as a host for insects, since no other species of tree is associated with so many species of insects: more than 50% of all insect species found in Great Britain live in the 20 000 hectares of wood pasture in the New Forest alone, and this landscape is habitat for a great variety of bird species, especially songbirds. These observations are clearly highly relevant to current issues of nature management, at the reserve and the landscape scales.

In Chapter 8, '**Frugivory in large mammalian herbivores**' by R. Bodmer and D. Ward, the focus is changed to tropical and arid regions. On the basis of a survey of 178 large herbivores species in tropical regions, the occurrence of frugivory is described across the range of stomach complexity in large herbivores, from simple to advanced, and in animals with different adaptations to seed predation, including strengthened jaws,

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elaborate dentition and digestive systems. The occurrence of frugivory is compared between tropical forest and savannas, and across the range of body mass in large herbivores. Biomass density (kg km^{-2}) of large herbivores with different diets is compared across habitat types. The impact of frugivores on ecosystem dynamics is a consequence of both seed dispersal and seed predation: the importance of frugivory by mammals in the dynamics of ecosystems is difficult to assess because most of the studies lack detail, and very few measure the vital rates of the tree populations. These issues are illustrated by case studies in two extreme habitats, tropical rainforests and the Negev desert. Resource use by four species of Amazon ungulates in north-eastern Peru is compared using both stomach and faecal samples. The striking differences between the ungulate species are discussed in relation to the physical characteristics of the seeds and the adaptations of the large herbivores.

Work in the Negev on the ecologically important and complex interaction between Acacia trees, bruchid beetles and ungulates (which are both important seed predators) shows that, as expected, when ungulates are present, seed dispersal increases, thus reducing competition for the seedlings from the parent trees. However, contrary to the idea that large mammalian herbivores reduce the impact of seed predation by consuming seed pods before they can be infested, the results of this study indicate that ungulate activity does not reduce the impact of the bruchid beetles on seeds. Very few seeds eaten by bruchids germinate, and many eaten by ungulates do: interestingly the germination rate of Acacia seeds eaten by herbivores increases with the body size of the herbivores. The dispersal of Acacia seeds by large mammalian herbivores seems to have affected and, perhaps controls, the distribution of different ecotypes of Acacia trees on a large geographic scale in the Middle East. In conclusion, browsing by ungulates at high densities, reduced the growth rates of the young Acacia, but did not inhibit juvenile Acacia escaping above the browsing level. Negative effects of browsing on juvenile trees may not translate into changes in tree demography because of the enhancement of seed viability and germination by mammalian herbivores.

Chapter 9, '**Large herbivores as sources of disturbance in ecosystems**' by **N. Thompson Hobbs**, suggests that herbivores might be profitably viewed as agents of disturbance, or events which alter resource availability or substrates, thereby causing abrupt changes in states and rates of processes. Trampling is an unavoidable disturbance of large herbivores since a large body mass is supported on four hooves, creating a large force per unit area on ground vegetation and soil. Trampling area increases

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allometrically with body mass, but so does home range. Population density therefore decreases allometrically with body mass, effectively cancelling any relationship between body mass and the proportion of home range trampled, which is fairly uniform at approximately 7% of the home range trampled each year. But, notes Hobbs, if proportionally more time is spent in certain communities with a small area, then trampling is concentrated in those communities and can affect up to 50% of the area which is actually grazed. This explains the often highly trampled condition around water holes, for example. The effects of trampling are diverse. On the one hand, trampling compacts the soil and reduces water infiltration, but if the soil surface is covered with a biotic crust, as is often the case in arid environments, then trampling increases water infiltration by breaking the crust. Bare, trampled areas are available for colonization by seeds which require exposure to mineral soil, creating a matrix for high, small-scale plant species diversity. Trampling also fragments litter leading to faster decay. Finally, trampled areas are often sites of high colonization by nitrogen (N) fixing cyanobacteria.

Patches of faeces and urine can also be viewed as disturbances since they represent very abrupt changes in nutrient availability from the surrounding areas, a point which echoes that made by Frank in Chapter 11. Approximately 2% of an animal's home range is in urine patches at any one time, but if the animal urinates in certain types of sites more often than at random, then, like trampling, the proportion of actually grazed area affected by urination is much higher than expected at random. Hobbs presents equations demonstrating that faecal N deposition increases linearly with plant N concentration and body mass while urine N deposition increases quadratically with body mass and plant N. Therefore, very large herbivores which graze high N forage will return most of their N to the soil as urine, which is more readily available to plants than faecal material since the latter needs to be decomposed by soil microflora. This in turn results in higher plant N, higher productivity, and a higher probability that the herbivore will subsequently graze the urine patch and surrounding area.

Herbivores also modify the occurrence of other disturbances, most notably fire, by reducing standing fuels of dead straw, thereby reducing fire frequency. Herbivores also selectively forage in burned areas of grasslands because of the higher N availability in grass after a burn, and so herbivores can also increase the recurrence interval between fires on a site as well. However, browsers in forested areas tend to avoid plants which produce resinous tissues with high content of volatiles. Since these plant