

Chapter 14

Managing Browsing and Grazing Ungulates



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14.1 Introduction

Browsing and grazing ungulates comprise a diverse guild of herbivores, including domestic species such as goats (*Capra aegagrus*), sheep (*Ovis aries*), cattle (*Bos taurus*), donkeys (*Equus africanus*), horses (*Equus ferus*) and camels (*Camelus spp.*) and wild species, such as cervids (deer, moose), equids (zebra, wild horses), and bovids (wildebeest, impala, buffalo, bison, etc.). They occur across most of the earth's landscapes from intensively managed, planted pasture systems to extensive pastoral transhumance systems, and sedentary and migratory wildlife systems with little or no management (Fig. 14.1). The current distribution of individual ungulate species depends upon their historical range, prevailing environmental conditions, human population densities and associated socio-economic factors, as well as the objectives of management, such as biodiversity conservation, tourism, subsistence, commercial livestock products and game ranching (Gordon et al. 2004).

Domestic ungulate species play a major role in food production and the economies of most of the cultures of the world, yielding around 20% of the world's total food production (FAO 2013). Similarly, the livelihoods of millions of rural people are dependent upon livestock that range from subsistence systems to commercial ranching operations in developed countries. Across the globe wild ungulates such as

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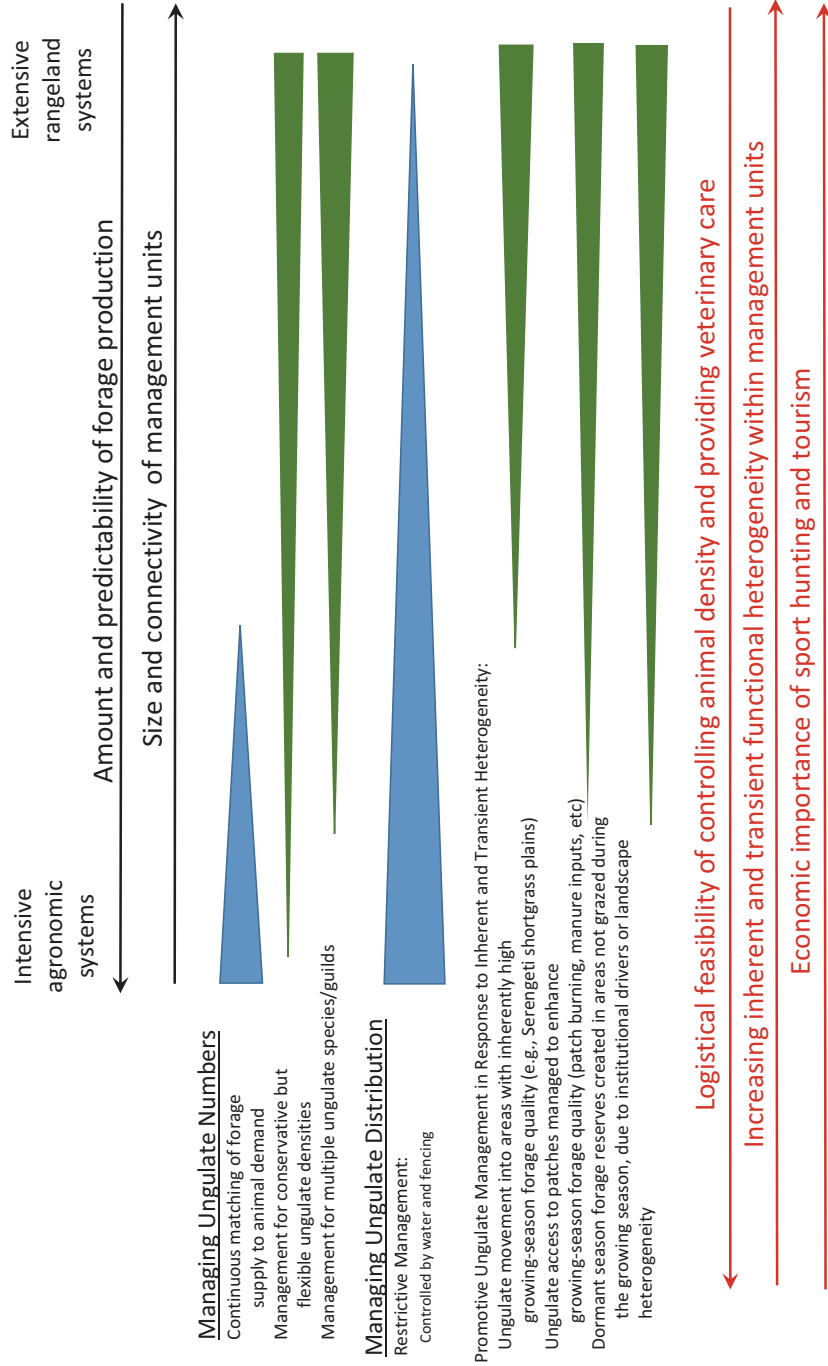


Fig. 14.1 Approaches to the management of ungulate abundance and mobility across a gradient from intensive agronomic systems to extensive rangeland systems, emphasizing the increasing importance of allowing ungulates to move in response to inherent and transient heterogeneity in extensive systems. Across this gradient, management emphasis shifts from restrictive management of ungulate foraging decisions in relation spatial heterogeneity

elephant (*Loxodonta africana* and *Elephas maximus*), wildebeest (*Connochaetes taurinus*), buffalo (*Syncerus caffer*), bison (*Bison bison*), elk (*Cervus elaphus*) and caribou (*Rangifer tarandus*) are important for tourism-based economies in many regions, including providing a prey base supporting iconic predators such as lion (*Panthera leo*), leopard (*Panthera pardus*), tiger (*Panthera tigris*) and grey wolf (*Canis lupus*). For example, wildlife tourism in Botswana contributed 11% to GDP in 2016 (WTTC 2017), in a country with a large beef industry as well as being the world's largest exporter of diamonds. Tourism in Tanzania is driven largely by its world-renowned wildlife, and is now the nation's leading economic sector, contributing 14% to GDP in 2014 (WTTC 2015). Yellowstone National Park, in the USA, attracted over 4.25 million visitors in 2016 (US National Park Service 2017). Apart from their economic importance, ungulates make up a large proportion of large mammal biodiversity and play an important role in shaping plant communities and ecosystem processes (Frank et al. 1998; Augustine et al. 2003; Augustine and McNaughton 2006; Fornara and Du Toit 2007; Mishra et al. Chap. 7). Their mobility requires conserving vast tracts of land, which is important for overall biodiversity conservation.

Having established the importance of browsing and grazing ungulates for livelihoods of people, and for biodiversity conservation, over a wide range of systems, from intensively-managed livestock systems to extensive migratory wildlife systems, and from arctic tundra to tropical savannas, an important question is whether there are some general concepts, and principles, that apply globally to their management? Here, we examine several concepts related to the ecology and productivity of ungulate populations and apply these concepts to their management. Central to the focus of this Chapter is the foundational role of resource heterogeneity in supporting ungulate populations, wild or domestic. The importance of resource heterogeneity for maintaining biodiversity, ecosystem processes and the productivity and stability of ungulate populations, is now well recognised (Illius and O'Connor 2000; Owen-Smith 2002, 2004; Augustine et al. 2003; Augustine and McNaughton 2006; Hobbs et al. 2008; Fuhlendorf et al. 2009, 2017; Fynn et al. 2015, 2016). In this Chapter we discuss the functional aspects of resource heterogeneity for ungulates, how this heterogeneity is distributed on ecological gradients, and temporally by disturbance, and the implications for management, at various scales.

14.2 Key Concepts Needed for the Management of Browsing and Grazing Ungulates

Ungulates require a balanced diet of energy, protein and minerals, which is rarely achievable at one given location (Prins and van Langevelde 2008). Moreover, overall intake requirements, and the components of a balanced diet, are not constant but vary seasonally with increasing demands for energy, protein and different minerals to support pregnancy and lactation (Murray 1995; Owen-Smith 2004; Prins and van Langevelde 2008). In addition, the quantity and quality of forage

varies over both space and time, and is closely linked to the density and distribution of ungulates. For example, large declines in available plant biomass, and its protein and energy content, over the dry or winter seasons, often lead to deficits in nutrient intake relative to maintenance requirements (Ellis and Swift 1988; Prins 1996; Frank et al. 1998; Owen-Smith 2008; Parker et al. 2009). All systems can experience periodic droughts or other forms of extreme weather events that, depending on the duration and on ungulate densities, can result in acute deficits in nutrient intake relative to maintenance requirements, leading to mortality and population collapses; these are, however, most common in arid and semi-arid regions (Walker et al. 1987; Ellis and Swift 1988).

In this Section, we provide a brief review of how heterogeneity of functionally-different resources enables ungulates to adapt to seasonally varying physiological and biophysical constraints on meeting nutrient intake requirements. We also review how herbivory may interact with heterogeneity to promote biodiversity.

14.2.1 Inherent and Induced Sources of Functional Resource Heterogeneity for Ungulates

Functional resource heterogeneity refers to spatiotemporal variability in forage resources, whereby different patches in the landscape vary in their probability of meeting the specific nutritional needs of a grazing or browsing ungulate over time (between seasons or years). The functional nature of forage resources may be characterized by spatial or temporal differences in the biomass, structure/height, phenology, species composition and nutrient or chemical properties of forage. These differences may be driven by soil, geological, mean annual rainfall or hydrological variation fixed in space (inherent heterogeneity), or by patchy effects of rainfall, fire or grazing across space and time (induced heterogeneity). Inherent forms of functional heterogeneity are generally associated with ecological gradients arising from topographic, edaphic, and climatic variability, at various scales—including regional—or landscape-scale variation in soil moisture/salinity, across rainfall or flooding gradients (Bell 1970; McNaughton and Banyikwa 1995; Hopcraft et al. 2010; Fynn et al. 2015; Raynor et al. 2017), or altitudinal/temperature gradients in North America (Festa-Bianchet 1988; Frank et al. 1998), Fennoscandia (Albon and Langvatn 1992; Marell et al. 2006) and Asia (Omer et al. 2006). High-quality forages, supporting ungulate growth and reproduction, are mainly found, seasonally, in the less productive regions of ecological gradients, such as low-rainfall, saline regions and uplands, where grasses are shorter and more digestible, and support higher concentrations of minerals for pregnant and lactating animals (e.g., Murray 1995; Grant and Scholes 2006; Fynn et al. 2014). A key point is that important minerals, such as Ca, Na and P, are not at sufficient concentrations in forage across the broad landscape so animals must find specific sites where the concentration of these minerals is elevated (Murray 1995; Prins and van Langevelde 2008). This

results in the migration of some species of ungulates to extensive saline regions at a regional scale (Murray 1995; Fynn et al. 2014), or movement on landscape catena's to saline patches (sodic sites) at a landscape scale (Grant and Scholes 2006).

More reliable dry/winter season forages are usually found in more productive regions of the gradient, such as lowlands, high rainfall areas and wetlands (Frank et al. 1998; Hopcraft et al. 2010; Fynn et al. 2015). Importantly, wetlands and high rainfall regions can provide green forage during the dry season when most landscapes support only dry, low-quality forage (Prins 1996; Hopcraft et al. 2010; Fynn et al. 2015). Thus, meeting maintenance requirements during resource-limited seasons, or extreme climatic events, requires access to forage resources in these more productive habitats (wetlands, lowlands and high-rainfall regions), that maintain adequate quantity and quality (Prins 1996; Owen-Smith 2002; Hopcraft et al. 2010; Fynn et al. 2015). When these areas are discrete, within the landscape, they are commonly known as reserve and key/buffer resources (Prins 1996; Illius and O'Connor 2000; Owen-Smith 2002; Hopcraft et al. 2010), and can be essential for reducing the rate of use of body stores and preventing mortality (Illius and O'Connor 2000; Owen-Smith 2002; Hopcraft et al. 2010). To summarize the salient points of the discourse so far, it appears that, in contrast to the commonly-held view of key resources being limited to dry season reserves of forage (Illius and O'Connor 2000), that there are two distinctly-different kinds of key resources, each acting on different demographic parameters: (1) high-quality wet season key resources, supporting animal growth and reproduction; and (2) adequate-quality dry season key resources, minimizing weight loss and mortality (see Selebatso et al. 2018).

Apart from functional heterogeneity being distributed in fixed locations across ecological gradients (inherent), it may also occur as transient (induced) heterogeneity through stochastic, patchy rainfall or fire events that stimulate growth of fresh, high-quality green forage, actively sought out by various ungulate species (Verlinden and Masogo 1997; Frank et al. 1998; Fryxell et al. 2005; Fuhlendorf et al. 2009; Sensenig et al. 2010; Mueller et al. 2011; Raynor et al. 2017). In addition, grazing and browsing by ungulates may remove older, low-quality grass or browse and stimulate fresh high-quality regrowth (Vesey-FitzGerald 1960; Fornara and du Toit 2007; Odadi et al. 2011), thereby increasing subsequent forage quality, and the weight gain of ungulates (Gordon 1988; Odadi et al. 2011). In some situations, ungulate foraging may even create grazing or browsing lawns supporting higher quality leafy forage (Augustine and McNaughton 2006; Verweij et al. 2006; Fornara and du Toit 2007; Anderson et al. 2010), where growth of new forage may be stimulated relative to ungrazed or unbrowsed areas (McNaughton 1985; Fynn et al. 2017; Fornara and du Toit 2007).

Functional heterogeneity of resources may also be facilitated by the diversity of plants in a landscape or the same patch. DNA metabarcoding has revealed a wide range of plant species, and a high diversity of taxonomically similar plants (e.g., grasses), in the diets of a wide range of ungulates (Kartzinel et al. 2015), indicating that ungulates rely on a varied diet to meet their daily nutritional requirements, among other needs (see Prins and van Langevelde 2008). A critical point, rarely recognised in the foraging ecology of ungulates, nor in optimal foraging

theory, is that ungulates may select a diversity of plant species, not only for energy gain or for nutritional purposes, but also, for medicinal purposes. For example, different plant species may contain different macro- and micronutrients needed for specific physiological processes, or contain chemical compounds with anti-parasite properties (Lange et al. 2006; Shaik et al. 2006; Moreno et al. 2012; Mengistu et al. 2017). In addition, intake of forage may be stimulated by consumption of plant chemical compounds counteracting toxins in forage that retard intake; some plant species may contain compounds that nullify the effect of specific toxins (Provenza et al. 2003), or by foraging on different plant species, each containing different toxins that are complementary, a ungulate may obtain greater overall intake than by foraging on only one species containing only one of the toxins but which has a detrimental effect at higher doses (Provenza et al. 2003). Thus exposure of livestock to a greater diversity of plants has been shown to increase intake and stimulate milk production (Meuret and Dumont 1999; Provenza et al. 2003; Agreil et al. 2006).

Different plant species also allow diet breadth expansion over the annual cycle, as an adaptive foraging mechanism, to seasonal variation in the quantity and quality of individual plant species (Owen-Smith 2002). For example, grazers and browsers may shift their diets between different plant species, which meet different metabolic and nutritional needs, over the day's foraging activities, and over the annual cycle (Agreil et al. 2006; Owen-Smith 2002). The mechanistic basis for these diets shifts by browsers or grazers, over the annual cycle, is best understood by translating plant species-level selections into functionally different resource types, known as generic functional resources (Owen-Smith 2002). A combination of restricted intake, high-quality and staple functional resources are critical for animal growth and reproduction, while reserve, bridging and buffer functional resources help to maintain intake during the dry season, and may prevent population collapse during droughts (Owen-Smith 2002). For example, African buffalo were observed, during the dry season in Lake Manyara National Park, to increase protein intake by foraging on short, high-quality, *Cynodon dactylon*, lawns around the lake (restricted intake resource), but required taller sedge grasslands (reserve resource) to meet their overall intake requirements (Prins 1996).

Heterogeneity in forage resources, at landscape and regional scales, plays a crucial role in creating adaptive foraging options for ungulates over the seasonal cycle, and is a key consideration for how management actions influence the role of ungulates, and their productivity within the system (Fig. 14.1). A critical factor influencing ungulate access to inherent and induced forms of heterogeneity (adaptive foraging options), is the spatial scale available for movement, as heterogeneity may occur over hundreds of kilometres, either seasonally (Frank et al. 1998; Hopcraft et al. 2010; Fynn and Bonyongo 2011; Mueller et al. 2011), or stochastically and unpredictably within seasons (Verlinden and Masogo 1997; Fryxell et al. 2005; Mueller et al. 2011). The relationship between adaptive foraging options and spatial scale has major implications for management of ungulates, from the conservation of mobile wild ungulate species, to management of domestic ungulates on ranches, which will be discussed in later sections.

14.2.2 *Anthropogenic Disruption of Functional Heterogeneity*

A factor that plays an important role in creating heterogeneity in ecosystems, that support ungulates, is distance to permanent water, which if large enough (>15–20 km), creates herbivory gradients and so called piosphere effects (Sianga et al. 2017). For intensively managed rangelands, the provision of water sources, at high density across the landscape, as well as the installation of fencing, can enable maximal utilization of forage by domestic livestock species (Fig. 14.1; Fuhlendorf et al. 2017), or reduce spatial variation in vegetation utilisation in wildlife systems (Sianga et al. 2017); however, they may jeopardise ecological function, and other desired ecosystem services, such as landscape-scale hydrology, grassland structural heterogeneity and native plant and animal biodiversity (Fuhlendorf et al. 2017). Also in wildlife systems, for example, in regions with large elephant populations, maintaining large proportions of the landscape >15 km from permanent water (the maximum foraging distance of elephants from water—see Wato et al. 2018) facilitates woody vegetation structural heterogeneity and plant diversity, thereby promoting faunal diversity (Sianga et al. 2017). Similarly, placement of a high density of artificial water points across the landscape, in Kruger National Park, enabled the spread of water dependent ungulates to areas far from permanent water (perennial rivers) (Harrington et al. 1999). This may have led to increased lion densities in these back country areas, and an associated loss of refuges from predation for roan (*Hippotragus equinus*) and sable antelope (*Hippotragus niger*), possibly resulting in collapse of their populations.

Similar to the effect of artificial water eliminating predation refuges far from water in the landscape, heterogeneity in the age of forest stands in North America can play a critical role in the interactions and dynamics of moose (*Alces alces*) and woodland caribou (*Rangifer tarandus caribou*). Clear cutting of forest stands stimulates regrowth of trees and increases browse availability for moose, whereas old growth forests, with their abundant lichens, support woodland caribou (Bergerud and Elliot 1986; Rettie and Messier 2000; Wittmer et al. 2005). Widespread logging programs, that homogenize forest age and structure, can promote moose populations by increasing their food resource and, more insidiously, increasing the abundance of wolves (*Canis lupus*) in former caribou habitat, leading to increased predation pressure and declining caribou populations (Bergerud and Elliot 1986; Wittmer et al. 2005).

Prior to the European settlers disrupting natural processes in North American grasslands, interactions between fire and grazing, by the large mobile bison (*Bison bison*), created structural and compositional heterogeneity in the vegetation, as herds moved in response to burning, the distribution of water sources and the temporal pattern of precipitation (Fuhlendorf et al. 2009; Allred et al. 2011; Augustine and Derner 2014). Currently, Western-based approaches to management of rangelands prevents the maintenance of grassland structural heterogeneity, in extensive regions of North and South America, as well as portions of other continents (i.e., land is

compartmentalized in small homogenous units, and fire and grazing are managed in a homogeneous manner); as a result undermining ungulate interactions with heterogeneity, with negative consequences for biodiversity (Derner et al. 2009; Fuhlendorf et al. 2009, 2017).

Another anthropogenic influence on functional heterogeneity is altering the density of ungulates, either by removing predators, increasing water availability or providing supplementary feeding. Research through the twentieth century clearly showed that the largest influence of mammalian ungulates on rangeland condition, and animal performance, depends on ungulate abundance, typically quantified, for livestock, in terms of stocking rate, or the number of animals per unit space and time (Heitschmidt and Taylor 1991; Holechek et al. 2004; Briske et al. 2008). The influence of stocking rate, or more generally grazing intensity, is identified as more important than the grazing management system (which alter the timing and distribution of animals) in determining rangeland condition (Briske et al. 2008). Perennial grasses require long recovery periods, after grazing, if they are to persist in the long-term, but this is not possible at heavy stocking rates, because of the rapid depletion of available forage, forcing premature utilization of rested paddocks (i.e., paddocks without grazing) (Holechek et al. 2004; Fynn et al. 2017). In heavily stocked wildlife areas, grassland is homogenized to a short grass state, eliminating taller grass forage reserves, leading to reduced rainfall-use efficiency of plants and/or population collapse of ungulates during drought (Walker et al. 1987; Irisarri et al. 2016). Similarly, increases in wild ungulate density, in response to predator extirpation, have substantial consequences for their effects on functional plant community composition (Augustine and McNaughton 1998; Ripple and Beschta 2004). Whilst this body of research has been focused mostly on domestic animals, and typically on small experimental units, it is clear that the impacts of grazing/browsing on grassland, savanna and woodland ecosystems is largely dependent on the number of ungulates per unit of space and time (Walker et al. 1987; Briske et al. 2008). The key message is that excessive ungulate densities can reduce grassland structural heterogeneity in landscapes, remove forage reserves, increase runoff and erosion during rainfall events, and degrade overall primary productivity (Walker et al. 1987; Augustine and McNaughton 1998; Ripple and Beschta 2004; Briske et al. 2008; Irisarri et al. 2016; Fynn et al. 2017).

14.3 Applying Key Concepts for Management of Browsing and Grazing Ungulates

Whether dealing with conservation strategies for wild ungulates, or the management of domestic ungulates by pastoralists or commercial ranchers, several key concepts stand out as important. Clearly incorporating inherent, and induced, heterogeneity at landscape and regional scales, into conservation and livestock management strategies, is needed if optimal conservation goals and livestock performance are to be

realized. Conservation strategies globally, and in Africa in particular, have not been successful in maintaining the historic large populations, densities and diversity of various wild ungulates (Harris et al. 2009; Craigie et al. 2010; Fynn and Bonyongo 2011). One of the principal factors underlying declines in African wildlife is that functional heterogeneity of resources required by ungulates, over the annual cycle, is distributed on various ecological gradients, often at regional scales (see Sect. 14.2.1). However, protected areas mostly do not encompass the full extent of these gradients (Caro and Scholte 2007; Harris et al. 2009; Craigie et al. 2010; Fynn and Bonyongo 2011). With rapidly-growing human populations and settlements, agricultural expansion, and the associated construction of water sources, fences and roads, these ecological gradients are becoming fragmented and ungulate management is becoming increasingly restricted to smaller regions of these gradients (e.g., Sayre et al. 2013), thus offering less functional heterogeneity; i.e., heterogeneity declines with increasing management intensity, and smaller management units (left-hand side of the gradient in Fig. 14.1).

Those protected areas that do encompass sources of heterogeneity, at multiple spatial scales (e.g., the Serengeti-Mara ecosystem in Africa, and the Greater Yellowstone ecosystem in North America), still support productive and stable ungulate populations, and diverse ungulate communities (Fryxell et al. 2005; Frank et al. 1998). These examples, buttressed by ecological theory (e.g., Owen-Smith 2002, 2004; Fryxell et al. 2005; Hopcraft et al. 2010; Mueller et al. 2011), indicate that maintaining large areas available for the movement of nomadic and migratory populations should be a key management objective for conservation outcomes in rangelands. For less mobile ungulates, that utilize resource heterogeneity across smaller landscapes areas, such as moose (Mueller et al. 2011) or Greater kudu (*Tragelaphus strepsiceros*) (Owen-Smith 2002), conservation of extensive unfragmented landscapes is less critical (Mueller et al. 2011).

In the Serengeti-Mara system, the combination of the National Park, and various surrounding wildlife management areas, collectively achieve sufficient land area under protection to encompass the full rainfall gradient, the principal factor underlying functional resource heterogeneity (both inherent and induced) in the ecosystem (McNaughton 1985; McNaughton and Banyikwa 1995). In most regions of the globe, sufficiently large areas, for effective conservation of mobile ungulates, will only be possible if local communities of people are involved in the management of greater conservation regions using a multi-stakeholder approach. It is becoming increasingly recognized that protected areas alone are insufficient to conserve biodiversity and that implementation of conservation activities, across larger landscapes, including multiple land uses, within which protected areas are imbedded, is a key strategy for conservation (e.g., Miller et al. 2012; Sayer et al. 2013; Fynn et al. 2016; Fuhlendorf et al. 2018).

In this regard, there are several flaws in the current reliance on wilderness-based conservation strategy (or “fortress conservation”), such as (1) not accounting for the major historic influence of humans in shaping ecosystems; (2) being conceptually deficient in approaches to biodiversity conservation in landscapes now dominated by humans; and (3) being responsible for fragmentation of larger, more functional

landscapes and ecosystems, by focussing conservation activities on small parts of these larger landscapes (Fynn et al. 2016; Fuhlendorf et al. 2018). Clearly, conservationists need innovative new approaches for the conservation of mobile ungulates, shifting emphasis from wilderness-based protected areas to approaches that promote connectivity across larger, more functional, landscapes in which protected areas are imbedded. Such an approach is possible with the understanding that conflict between wildlife, people and livestock is largely caused by an unfavourable spatio-temporal configuration of land use and livestock management, rather than primarily by human population growth; for example, changes from mobile pastoralism to sedentary ranching, can result in declining wildlife numbers, compared with pastoral areas, despite similar human population densities (Western et al. 2009; also see Keesing et al. 2018). Achieving productive populations of both wildlife and livestock, in larger pastoral landscapes, is possible if livestock management is based on ecological concepts aimed at promoting mobility and functional heterogeneity in the ecosystem (Fynn et al. 2016).

The theoretical basis for coexistence of livestock and wildlife, namely management approaches facilitating grassland structural heterogeneity, and a favourable spatio-temporal configuration of land use and livestock management across large landscapes (Western et al. 2009; Augustine et al. 2011; Fynn et al. 2016), is gaining empirical support (see Western et al. 2009; Shamhart et al. 2012; Tyrrell et al. 2017; Keesing et al. 2018). In a classic example of how ecological theory can be effectively applied for conservation of ungulate populations in human-dominated landscapes, grazing management committees, in a pastoral region of Kenya, set aside a core ungrazed area, providing a taller dry season reserve of grass (for both wildlife and livestock), surrounded by a heavily-grazed livestock area, that provides short higher-quality grass for short grass specialist wildlife species (Tyrrell et al. 2017). Impala, wildebeest and gazelles preferred foraging in the heavily-grazed livestock area during the wet season (facilitation of higher-quality short grass by livestock—see Gordon 1988; Fynn et al. 2016) but shifted their foraging to the ungrazed area during the dry season and drought periods (Tyrrell et al. 2017). This management approach creates structural heterogeneity similar to that observed on ecological gradients (Owen-Smith 2004; Hopcraft et al. 2010) and demonstrates the value of the structural heterogeneity concept for facilitating the co-existence of livestock and wildlife (also see Shamhart et al. 2012 for a North American example).

A key point from the Kenyan example is that local communities of people were able to maintain their traditional livestock-based livelihoods while conserving wild ungulate populations, which creates opportunities for additional income from tourism (community-based natural resource management—CBNRM). The effectiveness of biodiversity conservation in larger conservation landscapes will be determined by how well local communities are integrated into the management of, and benefit flows (ecosystem services and economic gains), from these larger landscapes; bottom up decision-making, and management processes, must replace traditional, top-down, command and control paradigms, where local people received few incentives to support conservation objectives, thereby fragmenting landscapes (Miller et al. 2012; Sayer et al. 2013; Fynn et al. 2016; Fuhlendorf et al. 2018).

The functional heterogeneity concept also provides a framework for planning water provision strategies, in protected areas, by ensuring that sufficient distance exists between water points to promote heterogeneity in vegetation structure and predation risk. Taking into account, for example, the maximum foraging range of around 15 km for bull elephants from water (and probably beyond the limits of most water-dependent ungulates) (O'Connor et al. 2007), artificial water points would have to be at least 45–50 km apart to create zones of refuge from herbivory of 15–20 km across. Such a strategy will promote reserves of forage for the dry season and droughts (Walker et al. 1987; Fynn et al. 2016), provide refuges from overuse for favoured plant species (O'Connor et al. 2007; Russell et al. 2011; Sianga et al. 2017), and refuges from predation for predation-sensitive ungulates (Harrington et al. 1999). Similarly, management of the scale and heterogeneity of clear felling of forests, will affect woodland caribou and moose habitat, and their interactions with wolves. In this system the coexistence of predators and their prey depends on a heterogeneous mosaic of old growth, low-predation-risk forests (low wolf density) favouring woodland caribou, and recently-felled forest with high browse availability favouring moose and their predators (e.g., Bergerud and Elliot 1986; Rettie and Messier 2000; Wittmer et al. 2005).

Clearly, management of natural ecosystems must consider the key processes contributing to vegetation heterogeneity, at various scales. Management can influence many variables underlying heterogeneity, i.e., protected area design relative to ecological gradients (Hopcraft et al. 2010; Fynn and Bonyongo 2011), the scale and heterogeneity of clear felling of forests (Rettie and Messier 2000), and the maintenance of large distance gradients from permanent water (Russell et al. 2011; Sianga et al. 2017). Additionally, induced heterogeneity can be created by using patchy fires regimes (Fuhlendorf et al. 2009), strategic grazing by livestock (Shamhart et al. 2012; Fynn et al. 2016; Tyrrell et al. 2017), and the creation of nutrient hotspots in landscapes through corralling of livestock (Muchiru et al. 2008; Augustine et al. 2011; Porensky and Veblen 2015). Creating greater heterogeneity in plant composition and structure across landscapes, not only increases the opportunity for adaptive foraging options for ungulates, but also increases niche diversity for biodiversity (Dermer et al. 2009; Fuhlendorf et al. 2009, 2017; Fynn et al. 2016; Sianga et al. 2017).

Knowledge of the availability of various generic functional resource types (Owen-Smith 2002), in relation to physical traits (body size, specialized mouth/tongue anatomy) and feeding type (browser, mixed or grazer) of different ungulate species, provides a mechanistic framework for conservation and management of ungulates. For example, large-bodied tall grass grazers, such as buffalo, are unable to obtain sufficient intake on heavily grazed lawns (a restricted intake resource for buffalo—Prins 1996), whereas wildebeest and gazelles can (a high-quality/staple resource for these short grass specialists), explaining the spatial separation of buffalo vs. wildebeest and gazelles across grazing intensity gradients (Bhola et al. 2012). Thus the generic functional resource concept provides a useful framework for facilitating conservation management decisions; for example, whether an ungulate

species could be successfully introduced to a particular region, or the effect that introducing livestock grazing to an area might have on various ungulate species.

Many pastoralists understand the distribution and role of functional heterogeneity across ecological gradients, and move their livestock seasonally and/or spatially, in a similar manner to the movement patterns of wild ungulates (e.g., right side of Fig. 14.1; Breman and de Wit 1983; Homewood 2008; Sayre et al. 2013; Fynn et al. 2015). Similar to the situation with wild ungulates, traditional movement patterns of livestock, along ecological gradients and across landscapes, have been greatly fragmented by human population growth, development, agriculture, privatization and fencing of land, formation of protected areas and colonial boundaries (Niamir-Fuller 1999; Homewood 2008; Western et al. 2009; Sayre et al. 2013). It is clear that pastoralists had insight into important ecological principles and have developed survival strategies for coping with variable and unpredictable rainfall (Breman and de Wit 1983; Homewood 2008; Sayre et al. 2013; Fynn et al. 2015).

Regional-scale pastoral movement strategies are likely to help livestock keepers cope with predicted increases in rainfall variability, and more frequent droughts associated with climate change (Ogutu and Owen-Smith 2003); large-scale movements allow access to drought (buffer) resources in high-rainfall regions, or in wetlands, and the ability to spatially track patchy rainfall events (Breman and de Wit 1983; Fryxell et al. 2005; Homewood 2008). With policy trends, in Africa, and elsewhere, leading to privatisation of land that is compartmentalised into smaller units (e.g., Western et al. 2009; Sayre et al. 2013), the ability of livestock keepers to adapt to increased variability under climate change is reduced, because they can no longer access the full range of functional resource types (generic functional resources), often distributed on regional-scale ecological gradients (see Sect. 14.2.1). With there being increased emphasis globally on development of 'climate-smart agriculture' (cf. Gordon et al. 2016), and resilient approaches to dealing with climate change, the evidence and concepts presented in this Chapter clearly indicate that policy actions need to be scaling up, rather than reducing the size of management units (see also Fryxell et al. 2005; Hobbs et al. 2008; Western et al. 2009).

The concepts of spatial scale of movement and adaptive foraging, in relation to functional heterogeneity, has implications for the management of livestock on commercial ranches as well. Rangeland science has been dominated by a paradigm advocating management that facilitates spatially uniform, and moderate, utilization of forage, which often results in uniformity of vegetation composition and structure at the landscape scale (Briske et al. 2008; Fuhlendorf et al. 2017; Sayre 2017). In order to facilitate more uniform utilization of rangelands, the rangeland management profession has promoted the use of an elaborate system of fencing and small paddocks (Sayre 2017), with the establishment and maintenance costs of these fences contributing to debt and capital depreciation, reducing profits (Knight et al. 2011). Another cost of the current paradigm is that, as described above, enclosing livestock in small paddocks restricts their ability to make foraging decisions in relation to functional heterogeneity on the property (including nutritional and medicinal resources). With these factors in mind, fundamentally different approaches to rangeland management are emerging, which aim to facilitate access

to functional heterogeneity through use of fewer, much larger, paddocks and through seasonal movements between short grazed, high-quality grassland during the growing period and taller, ungrazed reserves of forage for the dry season (Fynn et al. 2017). Thus this approach more accurately simulates the natural seasonal movements of ungulates, and the ecological principles underlying their foraging ecology, than complex multi-paddock systems with their regular forced movements of livestock. Prevention of grassland maturation, and associated loss of quality, through sustained season-long grazing of priority paddocks increases animal production (the grazing facilitation concept explicitly addressed; see Gordon 1988; Odadi et al. 2011), while taller reserves of forage, in ungrazed paddocks (rested the entire growing season), reduce weight loss and mortality during the dry season and droughts (Walker et al. 1987). The purported advantages of managing for uniformity, therefore, are questionable given that rangeland heterogeneity enhances adaptive foraging options for livestock and, consequently, their nutrition and production (Owen-Smith 2002, 2004; Hobbs et al. 2008; Hopcraft et al. 2010).

Access to functional heterogeneity is related to the spatial area available for movement (Hobbs et al. 2008), with the consequence that negative density-dependent effects on animal performance (Sandland and Jones 1975) may be weaker at larger spatial scales (Wang et al. 2006; Hobbs et al. 2008). This key ecological principle is disregarded (with negative consequences for animal health and production) by ranching systems favouring an elaborate system of fencing and regular movement of livestock between small paddocks (see Fynn et al. 2017). Forage, and habitat selection, are highly complex and not always based on maximizing energy and protein intake. Ungulates also need to balance protein, energy and fibre intake (e.g., Prins 1996), counter toxins in forage (e.g., Provenza et al. 2003), deal with parasites or any other medicinal requirements (Lange et al. 2006; Shaik et al. 2006; Moreno et al. 2012; Mengistu et al. 2017) and other reasons (e.g., avoiding cold winds, heat, insects, etc.). Giving livestock greater freedom to forage in large paddocks facilitates adaptive foraging choices and habitat use decisions, with obvious benefits for livestock production and health (Provenza et al. 2003; Fynn et al. 2017), provided that stocking rates are set appropriately (Briske et al. 2008). Patchworks of fire-modified vegetation can provide a valuable alternative to the use of paddocks on ranches (Limb et al. 2011). In more arid regions, surface water management provides a useful alternative to fencing for controlling the distribution of livestock.

14.4 Conclusion

The concept of functional heterogeneity is applicable to the management of both wild and domestic browsing and grazing ungulates at the full range of scales, from landscapes to regions, and from intensive small stock systems in Europe (Meuret and Dumont 1999; Agreil et al. 2006) to extensive transhumance and wildlife systems in Africa (Breman and de Wit 1983; Homewood 2008; Fynn et al. 2015), Asia (Omer

et al. 2006), North America (Festa-Bianchet 1988; Rettie and Messier 2000; Fuhlendorf et al. 2009) and Fennoscandia (Albon and Langvatn 1992; Marell et al. 2006). Facilitating access to, and maintaining, functional heterogeneity, therefore, should underlie the management and conservation of browsing and grazing ungulates, whatever the location, scale of management and animal type. It should be recognized, however, that the positive influence of functional heterogeneity is not independent of other key management factors. For example, negative density-dependent effects, due to excessive animal population size, can override the positive effects of, or even degrade, functional heterogeneity. Nevertheless, it is also true that the strength of the density-dependence effect increases with the decreasing area available for movement (decreasing management unit size; e.g., Wang et al. 2006; Hobbs et al. 2008). Consequently, appropriate management of browsing and grazing ungulates must explicitly consider their population size/stocking rate (increasingly relevant with decreasing management unit area), while facilitating access to functional heterogeneity, both spatially and temporally.

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