

4 Variability, Heterogeneity, Diversity and Productivity in Grazing Systems

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4.1 Introduction

This chapter poses a perennial question in ecology: what determines the abundance and diversity of species in grazing ecosystems? The context of this question is recognition that ecosystems provide a wide range of services, many of which derive from or are related to the system's diversity. For example, grassland and savannah biomes contribute significant amounts of all five of the ecosystem services (surface water supply, water flow regulation, carbon storage, soil accumulation and soil retention) examined in South Africa by Egoh *et al.* (2009). They found significant spatial overlap of ecosystem services with species richness (plants and animals) and vegetation diversity hotspots, consistent with the generally positive relationship between species richness and ecosystem functions at large scale.

Our focus is primarily on large vertebrate herbivores, and how the diversity and coexistence of these consumers may be related to the biodiversity and heterogeneity of the vegetation. We focus on the principles underlying diversity in diet optimization and resource use by herbivores, to examine how they exploit environmental heterogeneity and what effect this may have on species coexistence and abundance. We go to some lengths to

consider the consequences of climatic variability, which has profound effects on primary and secondary production, effects which may increase under some climate-change scenarios.

Although biodiversity has important connections with the provision of ecosystem services, the assessment of biodiversity is complex, and the most readily available measures rarely reflect the real attribute of interest for any particular role. For example, to measure biodiversity in terms of visible organisms, such as animals or plants, misses the much greater taxonomic diversity of microorganisms. These dominate the branches of the tree of life, and include most forms that are the main providers of most regulating and supporting services and are keys to many provisioning services. We acknowledge that there is far more to the biodiversity of grazing systems than meets the eye and than is represented by the macrofauna and flora.

McNaughton (1985) draws attention to several important properties of the Serengeti ecosystem, one of the most pristine, extensive and diverse of grazing systems: (i) variability in rainfall, and in the spatial distribution of nutrient availability, grazing and fire, is an inherent feature of many grassland ecosystems; (ii) the resulting pulses in plant growth produce a

shifting landscape of locally abundant but sometimes ephemeral forage resources; (iii) the mobility of grazers is essential to their ability to exploit such resources, consume a high fraction of primary production and become the dominant fauna; and (iv) grazers alter plant community composition and diversity, which may modify a host of ecosystem functions, and they can also modify forage quality, which may feed back on grazer abundance. McNaughton conjectured that grazers' abilities to buffer temporal stochasticity in primary production, by exploiting spatial heterogeneity and their modification of forage resources, 'produce a much more deterministic and stable grazing food web than would be expected in such a variable environment if vegetation productivity was less responsive to rainfall and grazing, the animals were sedentary, and community composition was uncoupled from its functional properties' (McNaughton, 1985, p. 282).

4.2 Temporal and Spatial Variability in Vegetation

As a food source for animals, vegetation has a number of shortcomings. It has a composition quite different from that of the consumer, much of it is indigestible even to commensal microbes, and the more nutritious components are sparsely distributed across the landscape. Allowing that ruminants are well adapted to coping with the first two limitations, the finding of sufficient food to meet daily and seasonal requirements remains a challenge.

4.2.1 Forage quality

The sources of variation in the quality of forage for herbivores are well known. Immature tissue consists mainly of metabolically active cell contents, which are almost completely digestible, but tissue maturation brings an increasing fraction of cell wall, itself becoming more lignified with age until less than half the forage is

digestible. Diversification of herbivore feeding niches arises from the differences in digestibility between plant parts and growth stage (such as newly emerged leaf, maturing stem or the twigs of browse species). These pose herbivores with significant opportunities and constraints on diet selection, and such differences are possibly greater than those offered by choice between plant species compared at similar growth stages. Immature plants take longer to crop than those that are more mature, but mature plants require longer digestive processing, so daily intake by herbivores is frequently a dome-shaped function of plant abundance (Fryxell, 1991).

Spatial heterogeneity in growing conditions affects plant species distribution and phenology. For example, savannah grasses growing in moister locations mature for longer and end up with more lignified and less digestible tissue, explaining why variation in digestibility is greater within species at the top and bottom of a catena than between species (Murray and Illius, 1996). At a landscape scale, there may be sufficient asynchrony in plant phenology to allow herbivores to exploit plants at peak nutritional benefit by ranging widely (Albon and Langvatn, 1992; Fryxell *et al.*, 2004; Mueller *et al.*, 2008; Holdo *et al.*, 2009).

4.2.2 Forage abundance

Most grasslands are subject to marked seasonality of production. Annual cycles of temperature or rainfall impose a cycle of plant growth and phenology that results in a cycle of food abundance and quality. Intra- and inter-annual climatic variability adds further to uncertainty in resource abundance, especially in arid and semi-arid tropical environments, where such variability is extreme. Production is closely related to rainfall, as demonstrated by Le Houérou (1984), and refined by Huxman *et al.* (2004), who derive similar estimates of rain use efficiency (RUE; annual above-

ground net primary production (ANPP) per mm of annual precipitation).

Grasslands showed greater inter-annual variability in ANPP than the other North American biomes examined by Knapp and Smith (2001), with coefficient of variation (CV) about 0.3 at the more arid sites. Drier grasslands are more variable than mesic or humid ones, for two reasons. First, the decreasing mean annual rainfall across a transect from humid grasslands to arid rangelands is associated with greater stochasticity in timing and size of rain events, with the result that the inter-annual CV of rainfall is inversely related to the mean (Davidowitz, 2002). The same has been shown for the resulting primary production, estimated in Argentine rangelands by remote sensing, there being an inverse relationship between the mean and inter-annual CV of normalized-difference vegetation index integrated over the year (NDVI-I) (Oesterheld *et al.*, 1998), with the most arid sites having a CV between 0.4 and 0.5. Second, the inter-annual variability of primary production has generally been found to be greater than the variability of rainfall in arid and semi-arid grasslands. For example, the analysis of 77 series of annual data on production and rainfall by Le Houérou *et al.* (1988) showed the variability in production to be, on average, 1.5 times greater than the variability in rainfall. Comparison of six North American grassland sites showed ANPP CV/rainfall CV ranging from 0.8 (i.e. ANPP is more stable than rainfall) to 1.8 (ANPP is nearly twice as variable as rainfall; Knapp and Smith, 2001). Over a 19-year time series at a semi-arid site in South Africa, with grass plots manipulated to have a species composition and basal cover representative of rangeland under grazing in 'good', 'medium' or 'poor' condition, the inter-annual CV of production was 0.57, 0.68 or 0.71, respectively, compared with a rainfall CV of 0.29 (Wiegand *et al.*, 2004). For ANPP to vary more widely than rainfall does requires some non-linearity or lag effects in the relationship between soil moisture and plant growth, and Wiegand *et al.* (2004) were able to demonstrate

'memory' effects of rainfall that 'amplified the variability in precipitation: production was higher during a sequence of several wet years or months and lower during a sequence of several dry years or months' (p. 256). The authors suggest that some grasslands may show shorter memory, which, combined with only short-term fluctuations in rainfall, would not tend to amplify annual variability in ANPP.

There is some evidence (Holm *et al.*, 2003, 2005) that grazing impacts on vegetation structure may reduce the response of primary production to rainfall and hence reduce secondary production, as proposed by Illius and O'Connor (1999). However, Palmer and Ainslie (2007) could find no change in the RUE implied by livestock numbers over a 75-year time series in a semi-arid pastoral region of South Africa, despite apparently radical modification of the vegetation by the conversion of rangeland to cultivated farmland. They attributed the resilience of livestock numbers to hotspots of grass production around homesteads and water courses. The absence of an external reference value for RUE under pristine conditions has often hampered interpretation of temporal trends, as in the ongoing controversy over whether the Sahelian grasslands are 'degraded' on the evidence of temporal changes in RUE (Prince *et al.*, 2007).

4.3 Diversity in Resource Use and Diet in Mammalian Herbivory

There is good evidence of diet optimization by herbivores, which show flexibility and adaptive changes in the selection of forage at the level of the plant part, phenological stage and vegetation community, and by their broader movement patterns and range use. Several decades of feeding studies well demonstrate that body size is the primary determinant of dietary options for mammalian herbivores. Large species, such as the plains bison or Cape buffalo, have broad muzzles and flattened dental arcades, are incapable of fine selection of specific plant tissues, but are able to meet

their nutrient requirements more readily from mature plant tissues than smaller species (Fryxell *et al.*, 2008). On the other hand, smaller herbivores are more efficient than large herbivores at picking out the more nutritious bits from highly heterogeneous plant communities. Coupled with the dome-shaped intake function that characterizes mammalian herbivores, allometric variation in foraging efficiency dictates that herbivores of different size tend to have different mixes of graminaceous versus herbaceous or woody browse in their diet, and different levels of vegetation abundance offer optimal rates of intake (Wilmshurst *et al.*, 2000; Fryxell *et al.*, 2008).

There is also evidence that mammalian herbivores tend to selectively graze patches that yield the highest energetic gain (Wilmshurst *et al.*, 1995; Fryxell *et al.*, 2004; Mueller *et al.*, 2008). Such variation in feeding constraints and consequently forage preferences creates ample opportunity for niche partitioning (Olf *et al.*, 2002; Fryxell *et al.*, 2008).

4.4 Herbivore Abundance: Landscape Structure and the Seasonal Constraints in Forage Resources

Herbivore biomass in natural grazing systems is clearly related to primary production. Fritz and Duncan (1994) showed that the 100-fold range in biomass density of the ungulate communities across 31 natural ecosystems in East and southern Africa can largely be explained by mean annual rainfall (taken as a proxy for primary production) and a classification of soil nutrient status into high, medium or low. Beneath this regional correlation of primary and secondary production lie sharp contrasts between the relative importance of the growing and dormant seasons in supporting and limiting herbivore abundance. Clearly, the growing season is when primary production occurs, but arguably the dormant season is the most critical time for the support of herbivore populations because that is when

forage is most likely to become depleted (Illius and O'Connor, 1999, 2000).

Inter-annual and spatial variability in primary production further complicate the relationship between plant and animal production. Populations of herbivores are likely to do less well in more variable environments. Davis *et al.* (2002) showed that variability in rainfall reduces the long-term growth rate of food-limited herbivore populations, and thus may determine whether or not populations persist. The simple reason for this is that the numerical response of herbivore growth rate to vegetation abundance is convex, and hence the effect of below-average vegetative growth exceeds the effect of above-average growth. There may be a similar asymmetry in the response of ANPP to rainfall: manipulation of the size and frequency of rainfall events showed that increasing the intra-annual variability of rainfall (but not its mean) increased temporal variability in soil moisture in grasslands, and ANPP lost during the longer dry periods was not fully compensated by the extra growth resulting from the wetter but less frequent rainfall events (Knapp *et al.*, 2002). Wang *et al.* (2006) showed that lower winter temperatures and increasing variability in winter severity strengthened the effect of density on elk and bison population growth rates. In contrast, the strength of density dependence was reduced by increasing spatial heterogeneity in vegetation, suggesting that access to heterogeneous vegetation allowed some buffering of temporal variability.

Mammalian herbivores can often persist, in spite of inter-annual variation in rainfall, by taking advantage of spatial heterogeneity in vegetation. Models of adaptive movement by Serengeti herbivores suggest that animal population viability may be dependent on access to resources that vary asynchronously over space (Fryxell *et al.*, 2005) and that free access sustains higher herbivore numbers than would otherwise be supportable (Holdo *et al.*, 2009). The same models suggest that herbivore mobility has cascading effects on other important properties,

such as the amount of combustible litter that can build up, woody vegetation cover and plant species diversity, all of which are important contributors to ecosystem services. Northern ungulates living in habitats with greater heterogeneity in elevation had shallower slopes in the relationship between per capita population growth rate and population density (Wang *et al.*, 2009). These studies provide evidence of a positive relationship between habitat heterogeneity and ecosystem carrying capacity for a given ANPP.

Highly variable primary production in rangelands has led some to take the extreme view that herbivore populations are not dynamically coupled to their resources (e.g. Behnke *et al.*, 1993). The concept of carrying capacity is discarded by this 'non-equilibrium' paradigm, because of the fluctuating resource base. Livestock populations are thought to have negligible feedback on the vegetation, as their numbers are reduced by episodes of drought-induced mortality. Degradation due to 'overgrazing' is thus held to be unlikely, as vegetation composition, cover and productivity respond primarily to rainfall. In a critique of this paradigm, Illius and O'Connor (1999, 2000) proposed that herbivore populations in climatically variable and spatially heterogeneous environments are regulated in a density-dependent manner by a particular subset of ('key') resources that are accessible in the dry season, while being largely uncoupled from the remaining, wet season resources. Generalizing from the perception of Scoones (1995) that livestock survival depends on access to 'key resource' areas during the dry season, Illius and O'Connor (2000) defined such resources in relation to the key factor. Given that the key factor determining animal population size is survival over the season of plant dormancy, key resources are those eaten then and whose abundance controls the strength of the key factor. Thus, reduced access to such resources would cause the population to decline. They further demonstrated that: (i) long-term mean herbivore abundance is very largely determined by the quantity of

key resources and scarcely at all by resources available in the growing season; (ii) the potential for grazing-induced transformation of the vegetation comprising the wet-season resource increases as the ratio of key resource to wet-season resource (and hence herbivore numbers) increases. The implications for managed or conserved ecosystems are that animal abundance and grazing impact are likely to be influenced markedly by the landscape's endowment of such key resources.

The implication of some subset of resources having a key role in herbivore population dynamics is, of course, that the remaining resources have a lesser or unimportant role. Thus, we can now begin to distinguish resources in terms of whether consumer population dynamics are coupled to them or not. Wet-season rangeland can be classed as a non-equilibrium resource, because the animal population's dynamics are not coupled to it. Superabundance of non-key resources is likely to be observed during the growing season, because the animal population is typically limited by scarcer, high-quality resources during the dormant season. Note also that the key and non-equilibrium resources need not be widely separated in space and may even occur on the same plant. Given a distribution of food quality, as described by Hobbs and Swift (1985), a consumer population will tend towards equilibrium with the quantity of resources above the minimum quality threshold, and will not be in equilibrium with the remaining (= non-equilibrium) resources below the threshold. Diet selection from heterogeneous resources will naturally cause the animal population's dynamics to depend differentially on different resources.

4.5 Herbivore Diversity and Productivity

What determines herbivore species richness in grazing systems, and does an increase in species richness increase secondary production? The effect of the structure of the community of herbivore consumers may well play a role in explaining why the

efficiency of energy transfer between primary production and secondary production increases with ecosystem productivity (slope > 1 , as shown in Fritz and Duncan, 1994).

African savannahs provide good evidence for the relationship between habitat and herbivore species diversity (reviewed by du Toit and Cumming, 1999). Herbivore species diversity follows the classic hump-shaped relationship with annual rainfall, a proxy of primary production (Olf *et al.*, 2002; Prins and Fritz, 2008). Olf *et al.* (2002) argued that the two components of food supply – plant productivity and plant nutrient concentration – have contrasting responses across gradients of precipitation, temperature and soil fertility. Increasing precipitation and temperature increase plant growth and lignification, leading to high biomass but low quality; richer soils allow increased nutrient concentration without inducing such rapid decrease in digestibility. The implication is that the highest potential herbivore diversity should occur in locations with intermediate moisture and high soil nutrients, because larger herbivore species tolerate lower plant nutrient concentration but require greater plant abundance (Olf *et al.*, 2002). It is the accumulation of medium-sized species that mostly contributes to the increase in diversity at the peak, raising questions about the mechanisms of coexistence. Murray and Baird (2008) also predicted, based on resource competition theory, the coexistence of a maximum number of species in environments with intermediate productivity. They distinguish species that compete by being the most efficient at acquiring the food that most limits their competitors (extraction maximizers) from those that specialize on the resource that most limits themselves (demand minimizers). Wildebeest are typical extraction maximizers, dominating plant communities by creating grazing lawns and excluding competitors, particularly in highly productive environments. Typical demand minimizers are morphologically diverse sympatric species exploiting different

niches due to a trade-off in size-related foraging efficiency (Murray and Illius, 1996; Croomsigt and Olf, 2006). Resource heterogeneity combined with different resource utilization thus creates the conditions for coexistence of species in grasslands, with species of smaller body size being dominant at low productivity and larger body size dominating at higher productivity. The differences in nutritive constraints with body size are also associated with differences in the scale at which species perceive and respond to resource heterogeneity in space and time (Ritchie and Olf, 1999). Spatial heterogeneity in resource distribution, generated by rainfall variability interacting with geomorphology and distance to water sources, promotes niche diversification, and hence diversity (du Toit and Cumming, 1999).

4.5.1 Different limiting processes for different components of the community?

Population limitation mechanisms may differ between species in a community. In particular, body size is likely to play a major role in setting the relative roles of predation and resource availability at the population level, hence the distribution of body sizes within communities may determine the relative importance of top-down and bottom-up controls in entire food webs. Accordingly, Hopcraft *et al.* (2010) proposed a general framework to predict the relative contribution of bottom-up and top-down controls on herbivores across environmental gradients, arguing that the functioning of savannahs is primarily determined by: (i) how vegetation quality and productivity directly influence the differential performance of herbivores of different body sizes; and (ii) how carnivores of different body sizes partition their food niches along a herbivore body-size gradient. Fritz *et al.* (2011) confirm the interplay between top-down and bottom-up forces in savannah systems by showing that: (i) predation could be limiting in most sites for small- and medium-sized ungulate species through the prevalence of size-

nested predation (i.e. the prey base of small predators is nested within that of larger predators); and (ii) in systems with non-migratory herbivores, the greatest consumption of primary production occurred in the system dominated by mega-herbivores, which are virtually free of predators. These results emphasize the importance of diversity in body size and morphology on ecosystem functioning, rather than species richness per se.

4.5.2 Diversity and the relationship between primary and secondary production

It may be expected from the **species complementary** framework that an increase in species richness makes more complete use of the primary production (Tilman *et al.*, 1997; Loreau, 1998). From an alternative viewpoint, **species functional redundancy** (derived from Neutral Theory; Hubbell, 2001) may result in there being no effect of increasing herbivore species diversity on secondary production. The former view is supported by Fritz and Duncan (1994), who found that species richness may marginally contribute to large herbivore biomass for a given rainfall, especially for low-nutrient sites. These are likely to be those with highest variability in space and time, and thus greater diversity of niches. Further analysis distinguishing between grazers and browsers showed that the metabolic biomass of grazers was not related to the number of species, while for browsers, species richness significantly increased the total metabolic biomass of the mesobrowser guild (Prins and Fritz, 2008). In fact, the number of species was the only explanatory variable for the metabolic biomass of mesobrowsers. For these sites, the overall browser biomass was only influenced by rainfall, as expected from the fact that the biomass of browsers is largely dominated by elephants and that elephant biomass is exclusively explained by rainfall (Fritz *et al.*, 2002). In showing that specialist browsers seem to be complementary in their use of their primary resources, we not only confirm

field observations about possible niche complementarity, but also suggest that systems richer in browsers may use primary production more thoroughly, at least in savannah-type ecosystems. These results further underline the necessity for accounting for the relative proportion of various body-size classes in ecosystem functioning, and, in particular, in relating primary production and secondary production.

4.6 Conclusions

Grazing systems involve herbivore populations exploiting plant resources whose composition is heterogeneous in time and space. Seasonal patterns of plant productivity and phenology cause wide variation in the abundance and nutritive value of forage over the year, and climatic variability generates wide inter-annual variation in primary production. Adaptive responses buffer the environmental heterogeneity in resource abundance, but seasonal bottlenecks in nutrition nevertheless regulate herbivore populations. By setting limits on herbivore numbers, seasonal bottlenecks define the aggregate herbivore impact on vegetation as well as determining herbivore community structure. Explaining how that impact is distributed across vegetation components in the landscape, and hence the way plant community composition is modified by herbivory, remains a significant challenge.

There is still poor empirical support for hypotheses about what constrains herbivore diversity, and how far herbivore and plant diversity influence each other. Herbivore species diversity is clearly related to plant species diversity in some studies of insects, which tend to have more specialized requirements than mammalian herbivores. But there is weaker evidence that mammalian herbivore community composition is a function of plant species diversity, and still less that secondary production is increased. In general, does herbivore diversity have any bearing on the services provided or is it enough to address

the maintenance of plant diversity alone? How will plant spatial heterogeneity and temporal variability be affected by climate change and are current conservation/management practices adequate to meet that challenge? Finally, what are the long-term costs associated with sustaining herbivore and plant diversity if, as increasingly seems likely, climate change significantly shifts species ranges?

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