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Grazer Ecology

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Introduction

Grazing systems, grass-like vegetation interacting with their large mammal grazers, are important globally, where estimates of their potential extent (depending on classifications) range from 30 to 70 percent of the terrestrial land surface and show a major presence on five continents. In grasslands and savanna ecosystems, the grazing energy channel is prominent (~50 percent of energy flows through herbivores), unlike energy flow in more arid ecosystems where the detrital energy channel predominates. While variable, estimates of consumption of above-ground net primary productivity (ANPP) by native large mammal herbivores ranges from 1 (desert grassland) to ~64 percent (mesic grasslands), and cattle remove 15–80 percent (see chapter by J. K. Detling, “Grasslands and Savannas: Regulation of energy flow and nutrient cycling by herbivores,” in *Concepts of Ecosystem Ecology: A Comparative View*, edited by L. R. Pomeroy and J. J. Alberts [New York: Springer-Verlag, 1988], pp. 131–154). Consequently, in addition to altered aboveground biomass, one expects significant system responses to grazers, including altered plant community species composition, changed plant morphology and population structure, impacted nutrient cycles, and altered habitat structure in turn affecting animal species distributions both native and exotic. Examples of each of these responses are provided in this article. Our bibliography takes a decidedly grazer-centric view. Topics in grazing ecology are wide ranging, where both plant and grazer responses are studied as we attempt to integrate the many moving parts operating at multiple scales to understand responses from multiple perspectives. These include an understanding of the role of disturbances (fire, drought, herbivory), internal dynamics driving fire-grazer interactions, variable environmental conditions (especially primary production and rainfall), resource heterogeneity at multiple spatial scales, variable herbivore body size, different digestive physiologies of herbivores, sedentary presence and migratory movement of large mammalian herbivores in response to variable environmental conditions, and trophic control of food webs including bottom-up/top-down regulation with important roles for direct and indirect species interactions. Combined, many factors contribute to a range of equilibrial and nonequilibrial interpretations of key responses and patterns of grazing ecology with important implications for management and conservation of these systems worldwide. Much of grazing ecology focuses on the interactions of large mammal herbivores with vegetation structure and plant communities. Much less is known about invertebrate grazers, although they can be important participants as well. This article deals primarily with vertebrate grazers, factors affecting grazing dynamics, and examples of the effects of grazing on grassland structure and function.

General Overviews

This section provides a fundamental description and recognition of the importance of grazing systems as described by several seminal papers, and we also provide critical references on the ecology and feeding physiology of large herbivore grazers. After providing descriptions of the general system and grazer participants, we include a subsection of alternate conceptual views of grazing ecosystems with implications for grazer management and conservation. Bell 1971 provides an overview synthesis of grazer interactions and species behavioral ecology based on native species within the Serengeti, which is then further developed in McNaughton 1985, McNaughton and Georgiadis 1986, and Sinclair and Norton-Griffiths 1995 provides foundational insights into the stochastic nature of grazer populations and ecosystem ecology of grazing systems, and the role grazers have on ecosystem function and structure within the Serengeti. Frank, et al. 1998 builds on insights from the African Serengeti and compares the quintessential African grazing system to Yellowstone National Park in North America. Burkepile 2013 makes a persuasive and call for the consideration of insights learned from both aquatic and terrestrial grazing systems to be synthesized to improve conservation and restoration of grazing systems generally. Given the central place of large herbivores for understanding the topic, additional references provide a framework for large mammalian herbivores and their ecology. Owen-Smith 1992, van Soest 1994, Gordon and Prins 2008, and Prins and van Langevelde 2008 are foundational books that give overviews of the importance of large herbivores to ecosystem ecology in grazing systems; provide insight on nutritional ecology of ruminants, behavioral ecology, and evolutionary biology of ungulates occupying grazing ecosystems; and introduce key questions on the interaction of grazers and their resources at varying spatial and temporal scales.

Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. ***Scientific American*** **225:86–93.**

Bell provides an important synthesis of a charismatic system on what was known about grazer communities at the time, especially regarding their synchrony with forage resources in space and time. Initial insights into forage maturation and nutritional ecology of wild ungulates are provided, triggering the development of key studies in this unique Serengeti ecosystem and elsewhere.

Burkepile, D. E. 2013. Comparing aquatic and terrestrial grazing ecosystems: Is the grass really greener? ***Oikos*** **122:306–312.**

The provision of examples of how herbivory in aquatic systems facilitates primary production, herbivore richness, competition, and facilitation as seen in terrestrial ecosystems is crucial for understanding grazer ecology. By showcasing studies that highlight our understanding of top-down versus bottom-up control and alternative states, this review establishes a framework in wet or dry ecosystems for determining drivers of grazer foraging choices, which inevitably should facilitate ecosystem conservation and restoration.

Frank, D. A., S. J. McNaughton, and B. F. Tracy. 1998. The ecology of the Earth’s grazing ecosystem. ***BioScience*** **48:513–521.**

Functional components of grazing ecosystems in the Serengeti (East Africa) and Yellowstone National Park (North America) are compared. Primary topics include energy dynamics, seasonal migrations and the role of nutrition-rich green waves, grassland structure and grazing efficiency, feedbacks, regulation of above-ground net primary productivity (ANPP) by grazers, sustainability of grazing systems, and human transformations and conservation challenges. Similarities and differences between these systems are examined in detail to seek general underlying patterns.

Gordon, I. J., and H. H. T. Prins. 2008. ***The ecology of browsing and grazing*****. Berlin: Springer.**

An evolutionary biology–focused book that introduces evolutionary history, morphophysiological adaptations, ruminant nutritional ecology, comparative feeding behavior and population dynamics, and management techniques of browsers and grazers as well as their effects on plant evolution and ecology.

McNaughton, S. J. 1985. Ecology of a grazing ecosystem: The Serengeti. ***Ecological Monographs*** **55:259–294.**

The grazing ecosystem in protected East African savanna (Kenya and Tanzania) is described with an emphasis on linking primary production and herbivory, including their critical interactions. Six general features emerge: (a) the stochastic nature of precipitation, grazing, nutrient availability, and fire; (b) fluctuations of primary production that produce an unpredictable food source for grazers; (c) nomadic lifestyles of mobile dominant grazers facilitate exploitation of constantly shifting resource base; (d) carrying capacity is not fixed independently of grazers because of their effect on primary productivity; (e) grazers influence the composition and diversity of vegetation; and (f) interactions lead to a more deterministic grazing food web than expected in such a variable environment.

McNaughton, S. J., and N. J. Georgiadis. 1986. Ecology of African grazing and browsing mammals. ***Annual Reviews in Ecology and Systematics*** **17:39–65.**

A crucial resource for understanding the differences between African browsers and grazers and their interactions with resources. Distribution, life-history strategies, and abundance of these mammals in relation to biotic and abiotic factors common in Africa are discussed. Authors also touch on the role of grazers as ecosystem engineers.

Owen-Smith, R. N. 1992. *Megaherbivores: The influence of very large body size on ecology*. Cambridge, UK: Cambridge Univ. Press.

This seminal book synthesizes studies in large herbivore ecology and most importantly raised questions on the role of body size in ungulate biology and the influence of megaherbivores on ecosystem processes.

Prins, H. H. T., and F. van Langevelde, eds. 2008. *Resource ecology: Spatial and temporal dynamics of foraging*. Wageningen UR Frontis Series 23. Dordrecht, The Netherlands: Springer Science & Business Media.

A book about the ecology of trophic interactions between grazers and resources. Key researchers in the fields of spatial ecology of herbivore resources, foraging ecology, movement ecology, and nutritionally ecology inform readers about resource ecology, and critical questions in grazer ecology are remaining to be answered.

Sinclair, A. R. E., and M. Norton-Griffiths, eds. 1995. *Serengeti: Dynamics of an ecosystem*. Chicago: Univ. of Chicago Press.

This is the first volume of a comprehensive, foundational series on the Serengeti grazing ecosystem and synthesizes the ecology, management, and conservation of the Serengeti ecosystem. The series progresses over a twenty-year period to continually update the areas of critical need and expands into the need to view the problem as a coupled human-natural system if the Serengeti is to be sustainable as a grazing system.

van Soest, P. J. 1994. *Nutritional ecology of the ruminant*. Ithaca, NY: Cornell Univ. Press.

This is a foundational text on nutritional ecology that highlights the importance of nutritional assessments to the ecology and biology of ruminants and other nonruminant herbivorous mammals. In turn, nutritional studies are placed in a historical context to highlight the effectiveness of nutritional approaches and their fundamental importance to issues of grazer conservation. Mechanistic causal interrelationships between plants and animals are emphasized.

Grazing Environments, Alternate Conceptual Models, and System Heterogeneity

Grazing systems occur throughout the world over a wide variety of environmental conditions and include a diversity of participant species. Dyksterhuis 1949 introduces the range model, which at the time was the first model to describe important perspectives on the composition of grazing lands and how they are to be maintained; this work set the stage for North American range management. Modern-day narratives of rules underlying grazing systems followed, including new frameworks for describing grazing systems and their functional properties in response to the relative roles of abiotic conditions, disturbances, grazing, and biodiversity. These views led to efforts to understand equilibrial versus nonequilibrial processes, as discussed in Westoby, et al. 1989; Illius and O’Connor 1999; Stringham, et al. 2003; and Briske, et al. 2005, and the significance of understanding multiple possible states in grazing systems in response to varying levels of grazing intensity and abiotic conditions. Efforts include thresholds between states introduced in Noy-Meir 1975 and tested in Porensky, et al. 2016. Coughenour 1991 reviews the significance of spatial heterogeneity of resources and habitats, including the appropriate spatial scale over which they operate. Coughenour 1991 provides a broad, initial overview of the importance of incorporating spatial aspects to plant-herbivore interactions in both native and livestock systems. O’Reagain, et al. 2014 reviews such interactions from a tropical grazing systems perspective. Brekke, et al. 2007 extends our understanding of abiotic conditions and grazing environments and how contemporary management needs to coordinate to minimize overgrazing and plan for stochastic resource availability. Together, these works highlight the importance of knowledge of past grazing land-management practices for informing contemporary management aimed at successfully maintaining spatial and temporal ecological processes that underlie grazing ecosystem structure and function.

Brekke, K. A., B. Oksendal, and N. C. Stenseth. 2007. The effect of climate on the dynamics of pasture-livestock interactions under cooperative and noncooperative management. *Proceedings of the National Academy of Sciences of the United States of America* 104:14730–14734.

This paper extends the “Tragedy of the Commons” argument by adding intrinsic (trophic self-regulation) and extrinsic (variable weather) properties to a model to assess human management of common resources when the carrying capacity varies. Overgrazing (original tragedy argument) and appearance of stable limit cycles make sustainable management difficult. Intertemporal coordination among herders can stabilize the system and maximize productivity when faced with temporally variable and unpredictable rainfall; lack of coordination leads to overgrazing and extensive fluctuations in resource availability.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives. *Range Ecology and Management* 58:1–10.

The authors synthesize current ecological contributions of ecological succession and grazing intensity in a multiple stable state context that underlie the development and application of state-and-transition models and thresholds as they affect rangeland health. The correct application of thresholds is critical but vexing because of the many interacting components and interpretations. Careful analyses and implications of key concepts including multiple states, thresholds, state-and-transition models, and rangeland health are provided, including suggestions for further development of ideas.

Coughenour, M. B. 1991. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *Journal of Range Management* 44:330–342.

This important synthesis sheds light on plant responses to animal movement from the minute tiller, patch grazing, and grazing lawn scale to the large-scale patterns such as herd rotation and natural migration. He discusses spatial herbivory patterns in ranching systems, traditional pastoral movement patterns, plant interaction with wild ungulate movement patterns, the cessation of wildlife migrations and associated cascading effects on grazing landscapes, and predators’ impact movement patterns.

Dyksterhuis, E. J. 1949. Condition and management of rangeland based on quantitative ecology. *Journal of Range Management* 2:104–105.

This paper introduced a Clementsian-based range condition and trend analysis (the range model), which defines range condition by its relative position along a successional gradient. The composition of a presumed presettlement climax community represented excellent range condition and served as a basis for judging grazing management. The paper recommends the use of permanent line-interception transects in critical areas as quantitative checks on the effectiveness of grazing management, which have served as starting points for many discoveries at the interface of grazing and community ecology.

Illius, A. W., and T. G. O’Connor. 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications* 9.3: 798–813.

This paper reviews the equilibrium/nonequilibrium paradigm debate that underlies the scope of management practices of grazing systems. Examples of interactions between plant and grazers within rangeland landscapes showcase when each paradigm best fits observed plant-grazer dynamics, especially by season. By highlighting the key resources concept with examples in African pastoral grazing systems, the authors demonstrate when equilibrial or nonequilibrial processes best match temporal forage availability.

Noy-Meir, I. 1975. Stability of grazing systems: An application of predator-prey graphs. *Journal of Ecology* 63:459–481.

Noy-Meir introduced Rosenzweig and MacArthur’s theoretical findings (1963) using basic Lotka-Volterra predator-prey models to the plant-herbivore literature. Specifically, insights on the stability and productivity of grazing systems using the threshold model (i.e., the ball and cup analogy) are introduced, insights that have anticipated many discoveries related to the equilibrium and nonequilibrium paradigms in rangeland/grazing ecology.

O’Reagain, P., J. Scanlan, L. Hunt, R. Cowley, and D. Walsh. 2014. Sustainable grazing management for temporal and spatial variability in north Australian rangelands—a synthesis of the latest evidence and recommendations. *Rangeland Journal* 36:223–

232.

This review integrates ecology into the management of Australia’s tropical tallgrass rangelands in response to rainfall variability. Management of stocking rates to avert risk associated with rainfall variability and its effects on pasture productivity and overgrazing is assessed. The use of grazing exclosures, adding watering points, and the use of patch burning can be important management tools for balancing uneven grazing distributions. Ecological shortcomings of multi-paddock rotational grazing relative to continuous grazing are discussed.

Porensky, L. M., K. E. Mueller, D. J. Augustine, and J. D. Derner. 2016. Thresholds and gradients in a semi-arid grassland: Long-term grazing treatments induce slow, continuous and reversible vegetation change. *Journal of Applied Ecology* 53:1013–1022.

North American northern mixed-grass prairie “state-transition models” might misrepresent the resilience of the ecosystem to grazing based on rates of plant community change under several realistic stocking rates. A thirty-three-year grazing intensity experiment quantified long-term plant community dynamics and plant community responses to grazing reversal treatments. Grazing does not cause difficult-to-reverse transitions between alternative stable states. A temporal gradient model in which grazing induces slow, continuous, and reversible changes in plant species abundance rather than discrete phases matches better.

Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2003. State and transition modeling: An ecological process approach. *Journal Range Management* 56:106–113.

The authors provide a framework for describing nonequilibrium responses in rangeland to natural or management-induced disturbances using state and transition models of alternate states to describe potential ecosystem dynamics. The importance of resistance and resilience for understanding the consequences of the model is discussed, and concise definitions for model components are provided.

Westoby, M., B. H. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266–274.

The paper overcomes the limitations of the range model with the development of state-transition models for vegetation dynamics in grazing lands. This work precipitated experiments geared to shape our understanding of terrestrial grazing system tolerance to grazing pressure, restoration potential, and overall resilience.

Fire-Grazing Interactions and the Structure and Function of Grazing Ecosystem

Fire is ubiquitous in many grasslands and savannas, including both natural fire and prescribed activities that vary in time and space. When important, the interaction between fire and grazing provides a critical template that structures grasslands and hence vegetation-grazer interactions. As documented by papers included in this section, the effects of fire-grazing interaction on grasslands are many and central. However, fire may not be a key process in all grazing systems worldwide as shown in Oesterheld, et al. 1999. In addition, studies from temperate and tropical grasslands and savannas reveal the importance of ecosystem-level processes in structuring grazing ecosystems by providing habitat openings, often (but not always) with reference to plant and animal species that coevolved with these processes, as emphasized in Knapp, et al. 1999; Fuhlendorf and Engle 2001; and Fuhlendorf and Engle 2004. Archibald, et al. 2005 emphasizes fire as a driver of grazer habitat selection in the context of grazing lawn development. Through structural equation modeling, Anderson, et al. 2007 documents the complexity of the roles fire and herbivory have in shaping the Serengeti ecosystem. In turn, Augustine and Derner 2014 shows that the impact of fire on grazer behavior is contingent on system productivity in a semiarid grazing ecosystem. Eby, et al. 2014 adds trophic interactions and links predation risk and body size as non–mutually exclusive factors driving grazer attraction to recently burned grassland. Collins and Calabrese 2012; McGranahan, et al. 2016; and Bielski, et al. 2018 couple the fire-grazer interaction with diversity-stability hypotheses to provide new questions and future avenues of research on this critical landscape-level disturbance.

Anderson, T. M., M. E. Ritchie, E. Mayemba, S. Eby, J. B. Grace, and S. J. McNaughton. 2007. Forage nutritive quality in the Serengeti ecosystem: The roles of fire and herbivory. *American Naturalist* 170:343–357.

Multiple interacting environmental influences explain savanna nutritional environments. Structured equation models including effects of fire; herbivory; rainfall; soil fertility; and foliar N, P, and Na examine direct and indirect paths affecting the nutritive quality of Serengeti savanna grassland. Overall changes in nutritive quality resulted from both altered foliar quality within species and changes in plant species composition. Fire frequency and herbivory often had offsetting but not equally balancing effects on nutrients, mediated through changes in plant species composition and abundance.

Archibald, S., W. J. Bond, W. D. Stock, and D. H. K. Fairbanks. 2005. Shaping the landscape: Fire-grazer interactions in an African savanna. *Ecological Applications* 15:96–109.

Burning and grazing interactions and the persistence of grazed patches were explored in South African savanna. Mowing increased grazing activity, and burned areas attracted herbivores from nearby unburned, grazed patches (ecological magnet effect); biomass lost to grazers recovered quickly after grazing. Fire history influenced grazing and grazing lawn distributions. Fire regulated the competitive balance between grazing-tolerant and intolerant grass species through grazing activity. Burning large areas could limit the extent of preferred habitat for grazers through loss of grazing lawns.

Augustine, D. J., and J. D. Derner. 2014. Controls over the strength and timing of fire-grazer interactions in a semi-arid rangeland. *Journal of Applied Ecology* 51:242–250.

This empirical study of fire-grazer interactions extends our understanding of grazer responses to recently burned range in more arid grasslands. An activity sensor data documented the number of times grazers spent feeding in burned and not-burned range. They also indicate the fire-grazer interaction only works in semiarid habitat when forage regrowth is possible.

Bielski, C. H., D. Twidwell, S. D. Fuhlendorf, et al. 2018. Pyric herbivory, scales of heterogeneity, and drought. *Functional Ecology*.

This paper identifies switches in the scales of feedback mechanisms from drought in grazing lands managed with fire. Drought decreases temporal stability in aboveground plant communities and removes the expected among-patch variability typically observed with patch-burn grazing. In contrast to positive feedbacks from fire and grazing that amplify aboveground biomass heterogeneity at landscape scales, drought promotes fire and grazing-driven heterogeneity at the within-patch scale. The expected negative feedback was not observed at the within-patch scale but rather at the landscape scale.

Collins, S. L., and L. B. Calabrese. 2012. Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *Journal of Vegetation Science* 23.3: 563–575.

Using data from long-term, watershed manipulations of fire and grazing, this paper summarizes how fire and bison grazing combine to affect the composition, structure (cover), and temporal stability of tallgrass prairie plant communities in topographically variable landscapes. Frequent burning favored dominance of C4 grass cover. Maximum plant species diversity and community stability are maximized primarily by bison grazing and periodic fire, with outcomes mediated by topography.

Eby, S. L., T. M. Anderson, E. P. Mayemba, and M. E. Ritchie. 2014. The effect of fire on habitat selection of mammalian herbivores: The role of body size and vegetation characteristics. *Journal of Animal Ecology* 83:1196–1205.

Effects of fire increase the potential nutritional quality of forage while reducing potential predation risk. This Serengeti National Park study describes the effects of fire on habitat selection by mammalian herbivore species that differ in body size. Total herbivore abundances were higher on burned areas; smaller herbivores preferred burned areas more strongly. Foliar nutrients increased in burned areas, and vegetation height decreased. Total herbivore and impala abundances reflected increased forage nutrition rather than reduced predation risk.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. *BioScience* 51:625–632.

The premise that grazing management enhances vegetation heterogeneity and will promote biological diversity on rangelands grazed by livestock is developed. Responses of wildlife species to traditional livestock grazing management that leads to homogeneous vegetative habitats is contrasted to approaches that promote heterogeneity, including the need to develop management that relies on fire-grazing interactions as a primary tool.

Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Ecological Applications* 41:604–614.

The authors link fire ecology with grazing ecology and demonstrate that these two disturbances are a key ecosystem-level process in grasslands when applied simultaneously to a grazing system. This fire-grazer interaction (“pyric herbivory”) has been shown to conserve or restore ecological pattern and process to grasslands through the creation of spatial heterogeneity at the landscape scale, with significant conservation benefits to a variety of animal species dependent on grassland habitat.

Knapp, A. K., J. M. Blair, J. M. Briggs, et al. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience* 49:39–50.

The keystone role of bison in North American tallgrass prairie in association with fire based on research at Konza Prairie Biological Station is reviewed. Primary topics include bison grazing activities and plant responses; factors affecting site selection of grazing sites by bison; other impacts of bison in tallgrass prairie, including nutrient redistribution, wallowing, and the impact of carcasses of dead bison; functional equivalency of bison and cattle; and conservation.

McGranahan, D. A., T. J. Hovick, R. D. Elmore, et al. 2016. Temporal variability in aboveground plant biomass decreases as spatial variability increases. *Ecology* 97:555–560.

An ecosystem-level fire-grazer interaction (“pyric herbivory”) is linked to temporal stabilization in grazing land aboveground biomass through the availability of high spatial variability in vegetation resources for grazers driven by the interaction of fire and grazing.

Oesterheld, M., J. Loreti, M. Semmmartin, and J. M. Paruelo. 1999. Grazing, fire, and climate effects on primary productivity of grasslands and savannas. In *Ecosystems of disturbed ground*. Edited by L. Walker, 287–306. Amsterdam, The Netherlands: Elsevier.

This chapter provides a quantitative and synthetic review of above-ground net primary productivity (ANPP) in grasslands and savannas as it varies along precipitation gradients accompanied by disturbance from fire, grazing, and climatic fluctuations. Grazing and fire effects on ANPP are much lower than precipitation, suggesting important compensatory mechanisms to explain the low contribution of grazing to observed variability in primary production. A conceptual model links the relative contributions of grazing, fire, and precipitation to ANPP.

Habitat Use, Distribution, and Movement of Grazers

Factors underlying the distribution, movement, and habitat selection of large mammal grazers at multiple spatial and temporal scales contribute significant insights to grassland structure and function. We break this section into two subsections: Patch Selection and Habitat Use, followed by Grazer Movement and Underlying Mechanisms. In each case, the papers selected identify how grazers use the environment spatially in terms of where they are coupled to the accompanying movement that explains their decisions.

Patch Selection and Habitat Use

Senft, et al. 1987 and Bailey, et al. 1996 review the multifactor dimensions affecting large mammalian herbivore habitat use and the behavioral mechanisms that underlie them. Senft, et al. 1987 also provides a useful conceptual hierarchy to think about foraging that can be evaluated at several scales in time and space. Fryxell 1991 and Wilmshurst, et al. 2000 establish and test models for understanding ungulate grazer patch selection for both migratory and sedentary species. Using Bayesian statistical approaches to occupancy modeling and remotely sensed forage availability data, Anderson, et al. 2016 (cited under Grazer Movement and Underlying Mechanisms) links body-size, predation risk, and a species affinity for high-quality foods to species associations and occupancy in a large African savanna.

Bailey, D. W., J. E. Gross, E. A. Laca, et al. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49:386–400.

This foundational paper synthesizes behavioral mechanisms that affect large herbivore distribution patterns as driven by foraging mechanics, diet, cognition, body size, and abiotic factors. It introduces the landscape grazing distribution model that provides a framework for evaluating the use of fine-scale foraging mechanisms based on spatial memory, which is currently being empirically studied in detail due to the advent of animal-borne GPS collars.

Edwards, G. R., J. A. Newman, A. J. Parsons, and J. R. Krebs. 1996. The use of spatial memory by grazing animals to locate food patches in spatially heterogeneous environments: An example with sheep. *Applied Animal Behaviour Science* 50:147–160.

Two grazing experiments show (1) the duration of time that sheep can still remember locations of patches with food, and (2) how sheep use experimentally placed cues near feeding stations to increase the rate at which they encounter preferred food patches, and exploit spatial heterogeneity in the food resource effectively.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* 138:478–498.

In formally introducing the “forage maturation hypothesis,” this paper presents an analytical model that unifies optimal foraging theory, nutritional ecology, and predator-prey relationships. It defines foraging optima at intermediate levels of biomass with resulting high plant quality as important for the development of movement ecology and the notion of migration as driven by resource surfing (i.e., the green-wave hypothesis).

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37:789–799.

This landmark paper identifies scale-dependent foraging processes that underlie decision making at the feeding station, plant community, landscape, and broad regional scales. While these processes are linked, the actual questions addressed at different scales are not the same, but all are important to fully characterize the foraging process. The relative importance of plant-herbivore interactions declines at large spatial scales as foraging decisions are increasingly involved in trade-offs with non-foraging ones.

Singh, N. J., N. G. Yoccoz, N. Lecompte, S. D. Cote, and J. L. Fox. 2010. Scale and selection of habitat and resources: Tibetan argali (*Ovis ammon hodgsoni*) in high altitude rangelands. *Canadian Journal of Zoology* 88:436–447.

Habitat (topography) and resource (feeding patch) by argali in a relatively homogeneous high altitude rangeland were assessed using ecological niche analysis, factor analysis (habitat selection), and biased-reduced logistic regression (selection of feeding patches); fuzzy correspondence analysis for vegetation categories; and micro-histological analyses for selection of plant groups. Argali preferentially selected an intermediate range of altitude, slope, and forage abundance, and feeding patch selection reflected a trade-off between forage quality and biomass.

Wilmshurst, J. F., J. M. Fryxell, and C. M. Bergman. 2000. The allometry of patch selection in ruminants. *Proceedings of the Royal Society B: Biological Sciences* 267:345–349.

This meta-analysis of patch selection data from Serengeti animals evaluates the trade-off in forage quality and quantity among small- to large-bodied ruminants and demonstrates energy gain optimization is a positive decelerating function of ruminant body mass. A gradient between optimal patch selection and body mass indicate similar-sized herbivores with similar feeding styles compete. Results also suggest large ruminants should perform better in productive grasslands, while small ruminants excel in low-productivity grasslands.

Grazer Movement and Underlying Mechanisms

De Knegt, et al. 2007; Riginos and Grace 2008; Mueller, et al. 2008; Singh, et al. 2010 (cited under Patch Selection and Habitat Use); and Anderson, et al. 2016 associate wild grazer distribution and movement to patch quality and patch type in open landscapes using different analytical approaches, while Allred, et al. 2011 and Raynor, et al. 2017 clarify the role of time since fire and the forage quality-quantity tradeoff in guiding large grazer habitat use in managed fire-dependent landscapes. Edwards, et al. 1996 recognizes the importance of grazer spatial memory in a controlled experiment, which is then extended to memory-based forage tactics at the landscape-scale with GPS-tracked wild bison in Merkle, et al. 2014. Advances in technology available to grazing-lands researchers have opened doors to many questions previously out of reach using traditional research protocols. Allred, et al. 2011 connects the movements of native and domestic grazers to the availability of recently burned habitat, offering high-quality forage through geographic information systems, statistical modeling, and GPS collars on bison and cattle. Ungar, et al. 2005 provides detailed advice on the analysis of ungulate activity data derived from GPS collars with activity sensors. Bailey, et al. 2015 introduces a technique for coupling grazer movement data to genetic information to determine livestock breed affinity for specific landscape features.

Allred, B. W., S. D. Fuhlendorf, D. Engle, and R. Elmore. 2011. Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution* 1:132–144.

Selection for sites of varying time since fire, topography, and distance to water of cattle and bison are compared at the landscape-scale within growing seasons. This study empirically links fire and grazing as a spatially explicit interaction that is motivated by the forage quality-quantity trade-off. Unlike fire and grazing as separate processes, this investigation confirms their interactivity as a driving ecosystem process that shapes the structure and function of mesic grasslands.

Anderson, T. M., S. White, B. Davis, et al. 2016. The spatial distribution of African savannah herbivores: Species associations and habitat occupancy in a landscape context. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371:20150314.

Habitat occupancy by large mammalian herbivores, carnivores, and environmental variation in African savannas was characterized using hierarchical Bayesian occupancy models. Size-dependent differences affecting habitat occupancy by animals were linked to normalized difference vegetation index (NDVI) (larger species) and recent burning (smaller species). A size-dependent woodland/riverine to grassland gradient resulted. Habitat occupancy was diffuse in large-bodied migrants and fine-grained by smaller taxa that preferred higher-quality patches. Lions were associated positively with large herbivore species and negatively with smaller taxa.

Bailey, D. W., S. Lunt, A. Lipka, et al. 2015. Genetic influences on cattle grazing distribution: Association of genetic markers with terrain use in cattle. *Rangeland Ecology and Management* 68:142–149.

Single nucleotide polymorphisms (SNPs) were used to genotype GPS-tracked cows in efforts to correlate genetic associations with grazing distribution across five ranches with extensive pasture habitat. A quantitative trait locus (QTL) was associated with the use of topography and distance traveled from water. Additional markers on separate chromosomes accounted for a substantial portion of the phenotypic variation in grazing distribution. These findings indicate grazing distribution can be inherited and highlight a new approach to associate genetic variation with cattle-grazing behavior.

de Knegt, H. J., G. M. Hengeveld, F. van Langeveld, W. F. de Boer, and K. P. Kirkman. 2007. Patch density determines movement patterns and foraging efficiency of large herbivores. *Behavioral Ecology* 18:1065–1072.

Movement patterns (levy walks [LW] and area-restricted search) of goats while foraging were characterized in response to density. At low resource patch density, LW models predicted foraging behavior (step length, turn angles, net displacement). At high patch density, foraging patterns more resembled area-restricted search and increased foraging efficiency.

Edwards, G. R., J. A. Newman, A. J. Parsons, and J. R. Krebs. 1996. The use of spatial memory by grazing animals to locate food patches in spatially heterogeneous environments: An example with sheep. *Applied Animal Behaviour Science* 50:147–160.

Two grazing experiments show (1) the duration of time that sheep can still remember locations of patches with food, and (2) how sheep use experimentally placed cues near feeding stations to increase the rate at which they encounter preferred food patches and exploit spatial heterogeneity in the food resource effectively.

Merkle, J., D. Fortin, and J. Morales. 2014. A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecology Letters* 17:924–931.

The authors empirically assess how grazers deal with uncertainty using memory and energy gains or the lack thereof to explain restricted space use. This study is one of the first to mechanistically link memory, energy gains, and restricted space use while establishing a fitness-based integration of movement, cognition, and spatial ecology of a large grazer.

Merkle, J., J. Potts, and D. Fortin. 2017. Energy benefits and emergent space use patterns of an empirically parameterized model of memory-based patch selection. *Oikos* 126:185–196.

This paper informs readers why memory-based grazing might have evolved, and how such behavior translates into restricted space use distributions. This study suggests energy intake will be lower for grazers with poor knowledge of the most profitable patch locations in the foraging area and demonstrates that what an individual animal remembers from many previous time steps will result in population-level spatial distribution in a landscape.

Mueller, T., K. A. Olson, T. K. Fuller, G. B. Schaller, M. G. Murray, and P. Leimgruber. 2008. In search of forage: Predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology* 45:649–658.

Dynamics of resource availability of Mongolian gazelles were examined to assess the foraging area required to meet nutritional needs. NDVI obtained using satellites images was an efficient predictor of gazelle presence. Gazelles preferred an intermediate range of primary productivity, reflecting a trade-off between quantity and nutritional quality seen in other studies. Areas with low NDVI were ingestion limited, and areas of high NDVI were digestion limited. Much spatial and temporal variability in habitat suitability was observed, requiring gazelles to range over large areas to meet nutritional needs.

Raynor, E. J., A. Joern, A. Skibbe, et al. 2017. Temporal variability in large grazer space use in an experimental landscape. *Ecosphere* 8.1: e01674.

Patterns of space use of female bison are evaluated with a focus on variation in fire frequency, topography, and previous-year forage production (fuel loads) in an experimental mesic grassland. Watersheds burned for the first time in several years experienced most use; coupling of grazer and postfire regrowth was only evident during a drought in a watershed that burned for the first time in four years; and low-lying areas wherefor regrowth is most likely to occur were more heavily used relative to upland areas during a drought.

Riginos, C., and J. B. Grace. 2008. Savanna tree density, herbivores, and the herbaceous community: Bottom-up vs. top-down effects. *Ecology* 89:2228–2238.

Habitat selection and foraging success by African savanna herbivores balanced maximizing forage (nutritional) intake and minimizing risk to predation. Structural equation modeling evaluated the influences of tree density on herbivores and the herbaceous community. Along a tree density gradient, cattle used the landscape relatively uniformly, wild herbivore preferred areas of low tree density, and elephants used areas of higher tree density. Top-down effects of predator avoidance are important, leading to cascading effects on savanna herbaceous vegetation.

Ungar, E. D., Z. Henkin, M. Gutman, A. Dolev, A. Genizi, and D. Ganskopp. 2005. Inference of animal activity from GPS collar data on free-ranging cattle. *Rangeland Ecology & Management* 58:256–266.

The methodology for obtaining ungulate time spent feeding and behavioral activity data from activity sensors on GPS collars is thoroughly explained. This method allows researchers to extract important information on animal time budgets as well as location-specific behaviors.

Grazer Effects on Grassland/Savanna Structure and Function

Grazers contribute to grassland structure and function in many ways. They can influence vegetation structure, plant community species composition, and species diversity, and affect ecosystem structure, productivity, and nutrient dynamics. In turn, these responses may affect the nature of the grazer-plant interaction, a point that emphasizes the recursive relationships involved. Two subsections highlight community-level responses affecting species level responses Grazer Effects on Vegetation, Heterogeneity, and Food Webs, followed by community aspects of ecosystem level responses Grazer Effects on Biogeochemistry.

Grazer Effects on Vegetation, Heterogeneity, and Food Webs

The effect of grazers on system responses may cascade and have effects on other taxa or on the spatial heterogeneity of resource distribution as showcased in western North America in Derner, et al. 2009. In addition, experimental studies using grazing exclosures and modeling efforts test processes inferred from observational studies. Adler, et al. 2001 compares actual data to simulated data on plant community response to grazing to provide a new geostatistical perspective on grazing and its effect on vegetation heterogeneity. Bakker, et al. 2006 highlights the interaction of habitat productivity and herbivore body size to modulate grassland plant diversity using long-term small-scale grazing exclosures across North America and Western Europe. Using the large-scale Kenya Long-term Exclosure Experiment (KLEE), Veblen and Young 2010 contrasts the effects of livestock and native ungulates on shaping vegetation heterogeneity in a savanna ecosystem. Chase, et al. 2000 exemplifies the use of long-term grazer exclosures for understanding food webs by quantifying plant species turnover as a component for elucidating bottom-up and top-down control of food web dynamics. Olff and Ritchieb 1998 sheds light on questions important to grazer effects on community structure and function by examining the role of herbivores in determining plant species diversity and discussing underlying mechanisms that may be at play in the process. Hempson, et al. 2017 determines native ungulate loss as a driver of woody encroachment and reduction in ecosystem services in African savannas by employing novel abundance data synthesis techniques. Irisarri, et al. 2014 demonstrates that livestock production is more efficient at consuming aboveground net primary productivity than natural systems, where livestock biomass is decoupled from natural variability in precipitation through management activities. Van der Plas, et al. 2016 shows how indirect effects from ungulate grazing, including “grazing tolerance” and “grazing resistance” hypotheses, predicted different grass traits leading to tall and short grasses. Together, these studies demonstrate the efficacy in well-designed experiments and analytical approaches in identifying processes that maintain grazing ecosystem structure and function.

Adler, P. B., D. A. Raff, and W. K. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128:465–479.

Variable degrees of spatial heterogeneity of vegetation structure in response to grazing is extensively reviewed. A cell-based simulation model is used to understand why grazing leads to increased spatial heterogeneity of vegetation structure in some cases and lowered levels in others, independent of exceptions from underlying soil conditions. Neighborhood interactions at the individual plant scale rather than disturbance events or underlying environmental heterogeneity may explain why homogeneous grazing dampens fine-scale spatial heterogeneity.

Bakker, E. S., M. E. Ritchie, H. Olff, D. G. Milchunas, and J. M. H. Knops. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters* 9:780–788.

Effects of primary productivity and herbivores size in grasslands are separated in an experiment from seven sites over a productivity gradient. Large herbivores led to increased plant species diversity at high productivity sites and decreased diversity at low productivity sites. Small herbivores did not show consistent effects on plant species diversity over this productivity gradient. Implications of results for grassland conservation are discussed.

Chase, J. M., M. A. Leibold, A. L. Downing, and J. B. Shurin. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology* 81:2485–2497.

Results from large herbivore exclosure experiments among grasslands assess trophic web structure and food web interactions along a productivity gradient to assess control. At low productivity, consumer effects are large and drop off as productivity increases, presumably because of compositional turnover in plant species with higher plant productivity. The degree of herbivore control of trophic structure in grasslands reflects the effect of herbivory on plant species composition. Results are discussed in the context of bottom-up and top-down control of food web dynamics.

Derner, J. D., W. K. Lauenroth, P. Stapp, and D. J. Augustine. 2009. Livestock as ecosystem engineers for grassland bird habitat in the western Great Plains of North America. *Rangeland Ecology and Management* 62:111–118.

This forum piece introduces the utility of livestock as ecosystem engineers and addresses potential benefits and consequences associated with heterogeneity-based management practices for conservation grazing in the semiarid rangelands of the western North American Great Plains. By taking scale into account, Derner and colleagues demonstrate cattle can be used to engineer habitat for secondary consumers, birds, by modifying vegetation heterogeneity within-pastures or among-pastures.

Hempson, G. P., S. Archibald, and W. J. Bond. 2017. The consequences of replacing wildlife with livestock in Africa. *Nature Scientific Reports* 7:17196.

Herbivore biomass losses in sub-Saharan Africa in wetter areas and biomass increases and functional type turnover in arid regions were recorded. Reduced herbivore abundance is linked to altered ecosystem processes (fire and expansion of woody cover). A conceptual model of herbivore community highlights shifts from diverse native herbivore communities to cattle- and goat-dominated communities concerning ecosystem services. Greenhouse gas emissions and diffusion of nutrients across ecosystems from daily and seasonal movements reflect the transition to livestock-dominated communities.

Irisarri, J. G. N., M. Oesterheld, R. Golluscio, and J. M. Raruelo. 2014. Effects of animal husbandry on secondary production and trophic efficiency at a regional scale. *Ecosystems* 17:738–749.

Net secondary production (NSP) of livestock from Argentina and global natural systems across a wide precipitation gradient test the hypothesis that management practices in agricultural grazing systems result in higher consumption, NSP per above-ground net primary productivity (ANPP), and higher trophic efficiency. For homeotherms, consumption was greater in agricultural versus natural systems, resulting in higher NSP. Homeotherm trophic efficiency (E_{troph} = NSP: ANPP) was higher and varied along a precipitation gradient in a nonlinear fashion. Interannual variation in NSP was lower in agricultural systems.

Olff, H., and M. E. Ritchieb. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* 13:261–265.

This review examines the role of herbivores in determining plant species diversity and discusses underlying mechanisms that may be at play in the process. Primary factors include the spatial scale of plant species richness considered, contributions of local colonization, extinction and competitive exclusion processes, the importance of herbivore type, the consequences of environmental gradients, and interactions among these factors.

van der Plas, F., R. A. Hiwison, N. Mpanza, J. P. G. M. Cromsigt, and H. Olff. 2016. Different sized grazers have distinctive effects on plant functional composition of an African savanna. *Journal of Ecology* 104:864–875.

A “Russian doll” grazing-exclosure experiment tested effects of different size classes of African grazers on vegetation structure and taxonomic composition. In response to indirect effects from ungulate grazing, “grazing tolerance” and “grazing resistance” hypotheses predicted different grass traits leading to tall and short grasses, respectively. Total herbivory had the strongest effects on vegetation structure, and plant species composition responded to grazer size classes, especially smaller meso-herbivores. White rhinoceros did not affect vegetation structure or plant community species composition.

Veblen, K. E., and T. P. Young. 2010. Contrasting effects of cattle and wildlife on the vegetation development of a savanna landscape mosaic. *Journal of Ecology* 98:993–1001.

Livestock corrals create significant vegetation heterogeneity in sub-Saharan Africa landscape mosaics, leading to wildlife hotspots. Direct and indirect effects of wildlife and cattle on two dominant grass species were examined in long-term exclosure manipulations with combinations of cattle, large ungulate, and megaherbivore wildlife. Large ungulate wildlife reinforced vegetation heterogeneity, while cattle and megaherbivores reduced heterogeneity because of foraging preferences for one of the dominant grasses. Facilitation in the wet season sometimes resulted.

Grazer Effects on Biogeochemistry

Grazers have critical roles in the transport and the maintenance of nutrients in ecosystems and may underpin biogeochemical processes in some regions of the world. Detling 1988 provides an overview of the role of herbivores in nutrient cycling and energy flow in grazing ecosystems. De Mazancourt, et al. 1999 links grazing-induced soil-N content to the optimization of plant production by grazing in a nitrogen-limited West African savanna with implications for the coevolution of plants and herbivores. Frank and Groffman 1998 investigates ungulate influence on soil nutrient dynamics and provides a look into the relative contribution of large herbivores to controlling grassland soil processes at Yellowstone National Park. Augustine and Frank 2001 demonstrates native migratory ungulates mediate soil-N spatial structure in areas they graze by top-down control over plant species diversity. Derner, et al. 2006 reports on grazing and whole-ecosystem carbon storage interactions at long-term experiments on an east-west precipitation gradient in the North American Great Plains. The resulting overgrazing of grasslands in response to slash-and-burn forestry in South American dry tropical forest ecosystems is shown in Schulz, et al. 2016 to negatively impact the ecosystems’ ability to store carbon when exposed to increasing cattle grazing intensity. Smith, et al. 2014 demonstrates that overgrazing by sheep can reduce a soil’s ability to store carbon using a landscape-scale grazing experiment in Scottish uplands. In an erosion-prone grazing system in northern China, Yong-Zhong, et al. 2005 suggests rotational grazing would likely improve conditions because continuous grazing increased erosion risk and reduced soil biological activity as well as soil organic C and N storage. With climate change predicted to increase CO_2 levels in the atmosphere, an understanding of the response of critical components for livestock production to altered climate and CO_2 levels is paramount; Augustine, et al. 2018 sheds light on this issue.

Augustine, D. J., D. M. Blumenthal, T. L. Springer, D. R. LeCain, S. A. Gunter, and J. D. Derner. 2018. Elevated CO_2 induces substantial and persistent declines in forage quality irrespective of warming in mixed-grass prairie. *Ecological Applications*.

Changes in the distribution of annual precipitation, mean annual temperature, and elevated CO_2 should affect productivity, species composition, and biogeochemistry, thus affecting the forage quantity-quality trade-off for ruminants. CO_2 enrichment and altered temperature studies on forage quality and quantity in a semiarid, mixed-grass prairie showed that dry matter digestibility and nitrogen content of three dominant forage grasses was minor over seven years. Increased CO_2 levels led to increased forage production with reduced forage digestibility and N content.

Augustine, D. J., and D. A. Frank. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. *Ecology* 82:3149–3261.

Scale-dependent soil-N and N-mineralization potential in response to native migratory ungulates at Yellowstone National Park was assessed. Patchiness was observed at small spatial scales (<2 m) in not-grazed areas; spatial heterogeneity was minimal in grazed areas. Diversified plant species from herbivory affected heterogeneity in soil processes; redistribution of dung and urine did not lead to soil homogeneity. At larger spatial scales, large herbivores led to detectable spatial structure in soil-N properties. No large-scale spatial structure in soil-N was observed in not-grazed sites.

de Mazancourt, C., M. Loreau, and L. Abbadie. 1999. Grazing optimization and nutrient cycling: Potential impact of large herbivores in a savanna ecosystem. *Ecological Applications* 9:784–797.

The authors examine grazing optimization from herbivory through the recycling of limiting nutrients from increased turnover rate and test whether steady state, grazing optimization hinges on losses of a limiting nutrient during recycling of plant detritus and not turnover rate. Ecosystem modeling examines N-losses during recycling of plant detritus in annual fires versus herbivores using data from a humid African savanna. Herbivore optimization is likely in this system because N lost through herbivores (urine and fecal redistribution) falls below critical thresholds.

Derner, J. D., T. W. Boutton, and D. D. Briske. 2006. Grazing and ecosystem carbon storage in the North American Great Plains. *Plant and Soil* 280:77–90.

Derner and colleagues find differential responses between shortgrass and the mid- and tallgrass communities concerning grazing and whole-ecosystem carbon storage at long-term field plots. Grazed sites in mid- and tallgrass communities had 8 percent lower whole-ecosystem carbon storage than ungrazed sites, whereas grazed sites at shortgrass communities had 24 percent more whole-ecosystem carbon storage than ungrazed sites. They posit this result was due to more humid systems having large soil organic carbon (SOC) pools than more arid systems that could buffer ecosystem carbon fluxes, lower root carbon/soil carbon ratios in mesic systems having limited effects on the size of the SOC pool, and the absence of grazing-induced variation in the relative proportion of C3 and C4 functional groups in the more mesic systems.

Detling, J. K. 1988. Grasslands and savannas: Regulation of energy flow and nutrient cycling by herbivores. In *Concepts of ecosystem ecology: A comparative view*. Edited by L. R. Pomeroy and J. J. Alberts, 131–154. New York: Springer-Verlag.

This book chapter reviews evidence examining the importance of grazers to regulating energy flow and nutrient cycling in grasslands and savannas. Differences in the importance of grazing among grasslands are evident for energy flow, but most studies also show the importance of grazers for nutrient cycling, acting through plant physiological effects in response to grazing.

Frank, D. A., and P. M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. *Ecology* 79:2229–2241.

Migratory ungulates and variable site conditions for grassland soil mineralization and nutrient dynamics in long-term exclosure experiments were studied over time at Yellowstone National Park. Net N-mineralization in grazed plots about doubled that of non-grazed plots; grazer enhancement of N-mineralization about equaled the maximum difference observed among fenced plots. Herbivores increased labile fractions of organic soil matter quality. The landscape influence on the microbial N-immobilization was much greater than grazing. Landscape-level effects on field N-availability is mostly due to microbial immobilization; the grazing effect was primarily stimulated.

Schulz, K., K. Voigt, C. Beusch, et al. 2016. Grazing deteriorates the soil carbon stocks of caatinga forest ecosystems in Brazil. *Forest Ecology and Management* 367:62–70.

Rotational grazing is important to soil and plant communities in maintaining biogeochemical processes in Brazilian forest grazing systems. These dry tropical forest ecosystems lose their ability to store carbon when exposed to increasing grazing intensity especially the upper 5 cm of the soil profile. Soil organic carbon stocks exposed to a slash-and-burn system of land use are susceptible to the detrimental impact of grazing.

Smith, S. W., C. Vandenberghe, A. Hastings, et al. 2014. Optimizing carbon storage within a spatially heterogeneous upland grassland through sheep grazing management. *Ecosystems* 17:418–429.

A landscape-scale grazing experiment in Scottish uplands dominated by tussock forming grass assessed grazing management of sheep to optimize stored carbon in soil and vegetation. Grazing reduced C-stocks stored in the dominant grass. Based on simulation output from an organic turnover model (RothC), SOC sequestration was expected to decline under current commercial sheep stock rates and increase with no grazing and low sheep grazing levels.

Yong-Zhong, S., L. Yu-Lin, C. Jian-Yuan, and Z. Wen-Zhi. 2005. Influences of continuous grazing and livestock exclusion on soil properties in a degraded sandy grassland, Inner Mongolia, northern China. *Catena* 59:267–278.

Vegetation and soil properties under continuous grazing and livestock exclusion were examined in strongly degraded sandy grassland of northern China. Continuous grazing led to decreased ground cover, accelerated soil erosion (wind), coarseness in surface soil, loss of soil organic C and N, and decreased soil biological activity. After livestock exclusion, soil organic C and total N concentrations increased slightly compared to continuous grazing. Rotational grazing should buffer ground cover and soil processes from degradation in this erosion-prone system.

Foraging Behavior and Diet Selection

Foraging behavior and diet selection by individuals is a central problem in grazing ecology, and understanding the rules of resource acquisition is fundamental. The subsection Diet and Nutrient Selection highlights critical studies addressing such key questions as the relative roles of energy/mineral nutrients in limiting and guiding diet selection and nutritional intake rates. In the subsection Energy/Time Limitation and the Forage Maturation Hypothesis, research emphasizing the impact of energy and time limitation on foraging and the forage maturation hypothesis is described.

Diet and Nutrient Selection

Owen-Smith and Novellie 1982; Spalinger and Hobbs 1992; Gross, et al. 1993; Laca, et al. 1994; and Shipley, et al. 1994 introduce the grazed forage availability trade-off, constraints posed by vegetation structure on processing rates, functional responses, and seasonal variability in food quality and a grazer’s ability to meet nutritional needs. Theoretical models are proposed in Owen-Smith and Novellie 1982; Spalinger and Hobbs 1992; and Gross, et al. 1993 while empirical evaluations of foraging by individuals in the field are presented in Bradbury, et al. 1996; Fortin, et al. 2002 (cited under Energy/Time Limitation and the Forage Maturation Hypothesis); Shrader, et al. 2006. Shipley, et al. 1994 and Kartzinel, et al. 2015 address a range of questions about body size, environmental factors, and resource-partitioning underlying foraging dynamics in time and resource-limited environments.

Bradbury, J. W., S. L. Vehrencamp, K. E. Clifton, and L. M. Clifton. 1996. The relationship between bite rate and local forage abundance in wild Thomson’s gazelles. *Ecology* 77:2237–2255.

Bite rates of Thomson’s gazelles in shortgrass plains of Kenya over an annual cycle were examined with reference to alternate predictions of the Spalinger and Hobbs (S-H) foraging model. Bite rates during the dry season were correlated with dry green biomass and protein densities (S-H Processes 1 and 2 foraging), which switched to a negative relationship in the early wet season (S-H Process 3 foraging), possibly because sward height may modulate bite mass and control the foraging process.

Gross, J. E., L. A. Shipley, N. T. Hobbs, D. E. Spalinger, and B. A. Wunder. 1993. Functional response of herbivores in food concentrated patches: Tests of a mechanistic model. *Ecology* 74:778–791.

Authors compare foraging observations of twelve species of mammalian herbivores across a range of body size to test how a mechanistic model of asymptotic regulation of intake rate in hand-assembled variations of food-concentration patches (Spalinger and Hobbs 1992) explains variance in food intake rate. This empirical study provides strong evidence that the hypothesis that competition between cropping and chewing is responsible for the Type II functional response in herbivore food intake.

Kartzinel, T. R., P. A. Chen, T. C. Coverdale, et al. 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences of the United States of America* 112.26: 8019–8024.

Species-specific diet composition, breadth, and the degree of diet overlap and resource partitioning of coexisting large mammalian herbivores (LMH) in semiarid African savanna was assessed using DNA barcoding. Diets differed among all species comparisons; dietary overlap was most similar among species that were the same size, crossing grazer-browser guilds. Resource partitioning and plant species diversity may play a more important role for LMH coexistence than was previously believed.

Laca, E. A., E. D. Ungar, and M. W. Demment. 1994. Mechanisms of handling time and intake rate of a large mammalian grazer. *Applied Animal Behavior Science* 39:3–19.

This is one of the first studies of foraging kinetics in cattle using experimental swards. Results from this work are routinely used to parameterize large grazer intake rate models in investigations of grazing behavior.

Owen-Smith, N., and P. Novellie. 1982. What should a clever ungulate eat? *American Naturalist* 119:151–178.

This model evaluates the optimal diet range for various target nutrients and for consumers with time-minimizer or profit-maximizer tactics with resulting foraging performance sensitivities due to the forage quality-quantity trade-off. Subsequent studies of bite dimensions, nutrient assimilation under plant architectural constraints, and the role of patch structure scale follow from this fundamental work.

Shipley, L. A., J. A. Gross, D. E. Spalinger, N. T. Hobbs, and B. A. Wunder. 1994. The scaling of intake rate in mammalian herbivores. *American Naturalist* 143:1055–1082.

The authors provide a test of the integration of morphology (tooth size and jaw musculature) and mechanics (cropping and chewing processes) to explain the scaling of intake rate with body mass. Scaling of intake coincides with the scaling of daily energy requirements based on examining both responses from foraging observations of herbivores across a range of body sizes in Gross, et al. 1993 and thirty-nine published observations of short-term intake rate.

Shrader, A. M., R. N. Owen-Smith, and J. O. Ogatu. 2006. How a mega-grazer copes with the dry season: Food and nutrient intake rates by white rhinoceros in the wild. *Functional Ecology* 20:376–384.

This study demonstrates the ability of a large grazer to adjust food intake rate and nutrient gains to meet nutrient demands under varying environmental conditions. Using empirical measurements of bite mass and rate, this work uniquely shows that adjustments in forage intake or diet breadth was not sufficient to meet these demands. The mobilization of dry season fat reserves was required to meet nutritional needs.

Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: New models of functional response. *American Naturalist* 140:325–348.

The authors evaluate the use of alternate predator functional responses to explain herbivore foraging tactics. The use of a mechanistic model on three types of plant patch structure reveal that searching for food while simultaneously processing bites accounts for the Type II functional response frequently seen in herbivores.

St-Louis, A., and S. D. Côté. 2012. Foraging behavior at multiple temporal scales in a wild alpine equid. *Oecologia* 169:167–176.

A hierarchical approach to foraging by the nonruminant kiang in Tibetan highlands assesses how food limitation (quantity and quality) affects (a) instantaneous forage intake rate (bite size and functional responses) and (b) foraging behaviors at larger spatial and temporal scales in response to variable vegetation quality and quantity. The study illustrates the need to evaluate foraging behavior at multiple scales in response to the availability of quality food resources.

Energy/Time Limitation and the Forage Maturation Hypothesis

Studies in grazer foraging behavior, such as Fortin, et al. 2002, undertake experimental evaluations of instantaneous intake rate among swards varying in biomass (energy) availability. Such studies provide an understanding to the energy maximizing versus time-minimizing strategies used by grazers and provide insight into what landscape scenario (see Hebblewhite, et al. 2008; St-Louis and Côté 2012, cited under Diet and Nutrient Selection; Raynor, et al. 2015; Raynor, et al. 2016) or body size (see Shipley, et al. 1994, cited under Diet and Nutrient Selection) may be most likely to favor one strategy over the other. Initial theoretical (see Spalinger and Hobbs 1992, cited under Diet and Nutrient Selection) and later empirical work in Bergman, et al. 2001 and Drescher, et al. 2006 demonstrated that grazing is a behavioral process where animals can search for food and ingest food simultaneously. The recognition of this foraging tactic advanced our understanding about how optimal foraging theory traditionally associated with carnivores or predators that search and feed in an exclusive manner pertains to the ecology of mammalian herbivores.

Bergman, C., J. Fryxell, C. Gates, and D. Fortin. 2001. Ungulate foraging strategies: Energy maximizing or time minimizing? *Journal of Animal Ecology* 70:289–300.

By evaluating bison response to varying levels of forage quality and availability at feeding stations, this important experiment tests energy-maximizing and time-minimizing strategies to explain currency choice. Tests of foraging in response to patches of varying quality and quantity revealed bison preferred patches of high forage availability in order to minimize daily foraging time.

Drescher, M. I., M. A. Heitkonig, P. J. van den Brink, and H. H. T. Prins. 2006. Effects of sward structure on herbivore foraging behavior in a South African savanna: An investigation of the forage maturation hypothesis. *Austral Ecology* 31:76–87.

The forage maturation hypothesis (FMH) assumes that the temporal dynamics of forage quality and quantity feedbacks affects foraging and predicts foragers will select patches of intermediate forage quantity to maximize daily intake rate. Predictions of FMH hold based on cattle foraging in a spatially heterogeneous array of swards with complex vegetation architecture. The maximum intake rate was somewhat greater than that seen in studies using monospecific patches. Data on foraging behavior is linked to specific vegetation attributes.

Fortin, D., J. Fryxell, and R. Pilote. 2002. The temporal scale of foraging decisions in bison. *Ecology* 83:970–982.

This study tests the classical foraging theory assumption that animals maximize long-term energy intake rates. By carrying out field measurements across time periods spanning the dormant season to peak growth, results demonstrate that choice of forage items was more consistent with maximization of short-term than of long-term energy intake. This field study revealed temporal scale-dependence in rate-maximizing of foraging animals, which indicated that researchers should reconsider using a single rate-maximizing model to predict animal intake rate in foraging studies.

Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* 78:141–166.

The forage maturation hypothesis (FMH) is examined for migratory and nonmigratory elk in the Canadian Rocky Mountains over three spatial scales (study area, within home range, along movement path). FMH holds for both groups at all scales except for migrants at the local scale. Migrant elk realized 6.5 percent higher digestibility in diets than for residents, with greater individual performance. Migratory elk have greater access to higher-quality forage resulting from large-scale selection patterns as predicted by FMH.

Raynor, E. J., A. Joern, and J. M. Briggs. 2015. Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. *Ecology* 96:1586–1597.

This study evaluates the feeding station scale of the foraging hierarchy (Senft, et al. 1987, cited under Patch Selection and Habitat Use); it examines how foraging kinetics associated with transient maxima in forage quality and forage maturation influences the fire-grazer interaction. Instantaneous intake rate in tallgrass prairie watersheds burned frequently (one to two years), infrequently (four to twenty years), and not burned reveal crude protein intake is maximized in watersheds burned for the first time in four to twenty years.

Raynor, E. J., A. Joern, J. B. Nippert, and J. M. Briggs. 2016. Foraging decisions underlying restricted space use: Effects of fire and forage maturation on large herbivore nutrient uptake. *Ecology and Evolution* 6:5843–5853.

Bison foraging site selection in recently burned grassland is associated with crude protein intake optimization and the availability of feeding stations with high forage digestibility (low-to-intermediate biomass), as predicted by the forage maturation hypothesis (FMH; Fryxell 1991, cited under Patch Selection and Habitat Use). Net daily protein intake is optimized in the postfire period by grazing in recently burned grassland that then decays over the growing season. A weakened ability to optimize nutrient intake in recently burned grassland is linked with reduced restricted space use of recently burned grassland and the onset of warm season grass senescence.

Grazer Community Assembly and Species Interactions

As in most community studies, there is great interest in understanding the nature of species coexistence, species diversity, community assembly, and interactions among species in grazing systems. Because food resources in grazing systems are not particulate and because herbivory does not necessarily kill vegetation, the herbivore grazer-resource interaction is different structurally in an ecological sense than that described by classical optimal foraging theory. Subsections are included here to assess how species co-occur in communities: the role of Forage Quality and Environmental Gradients and Consumer Interactions in Food Webs.

Forage Quality and Environmental Gradients

Although many coexisting plant species in grazing systems could serve as unique resources to facilitate resource partitioning and species coexistence of grazers, plant species identity seldom plays this role, as coexisting large grazers often exhibit widely overlapping diets as described in Cromsigt and Olff 2006 and Cromsigt, et al. 2009. Hopcraft, et al. 2009 describes how variable vegetation structure and foliar nutritional quality seem to play more important roles in modulating grazer species interactions. Responses to predation risk can influence community assembly and species interactions. In a survival analysis of ten ungulate species, Owen-Smith, et al. 2005 shows many grazers are at risk to large predators to argue that bottom-up processes are not always the best explanations for species co-occurrence. Patch selection to minimize predation risk can alter where individuals forage, leading to foraging activity in suboptimal patches with respect to maximizing nutritional intake, but at a location where this is the best that they can do. The spatial heterogeneity of resources and habitat available to coexisting species is a final critical ecological dimension affecting species interactions and coexistence, a factor that is becoming more important as humans modify landscapes. Repeatedly, studies have shown that increased spatial heterogeneity of key resources (nutrition or habitat structure) results in increased species diversity. Herbivory by large mammal grazers and fire-grazing interactions often alters habitat structure, leading to increased species diversity. Fryxell, et al. 2005 and, at a larger spatial scale, Hempson, et al. 2015 employ expansive data sets of large herbivore movements and abundance in Africa to explore such interactions. Often missing from such studies is an understanding of the range of critical mechanisms underlying these responses, such as edaphic factors underlying plant communities (see Arnold, et al. 2014), in part because there are so many context-dependent responses with both top-down and bottom-up regulation operating in tandem. In addition to strictly nutritional dimensions, Sensenig, et al. 2010 and Goheen, et al. 2013 suggest that grazer body size can play an important role in understanding patterns of coexistence, in part because of differential nutritional needs and grazing constraints of species that differ in size. For example, small grazers can have difficulty feeding in tall vegetation and may require higher-quality food, so recent fire or the presence of grazing lawns may determine the size distribution of species in a grazer community.

Arnold, S. G., T. M. Anderson, and R. M. Holdo. 2014. Edaphic, nutritive, and species assemblage differences between hotspots and matrix vegetation: Two African case studies. *Biotropica* 46:387–394.

Are grazing hotspots associated with distinct plant species assemblages and soil fertility in Kruger (South Africa) and Serengeti (Tanzania) national parks? Clear differences in foliar-N within species were found with no differences in soil, soil-plant variables (N mineralization potential or mycorrhizal inoculation levels), and only weak shifts in community composition. Results contrast with sites showing a long history of livestock concentrations, where edaphic factors correlate strongly with hotspots. Grazer-plant interactions are more likely to maintain hotspots than soil-plant interactions at such sites.

Cromsigt, J. P. G. M., and H. Olff. 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: An experimental approach. *Ecology* 87:1532–1542.

This large-scale field experiment assessed whether larger species that forage at a coarser scale tolerate lower-quality food than is seen for smaller species, as predicted by a fractal model. Natural visitation rates by herbivores of different sizes to an experimental matrix that manipulated grain size with mowing and quality of patches (fertilizer) was followed. Foraging differences were observed with respect to grain size and foliar nutritional quality, outcomes that may contribute to resource partitioning by savanna ungulates.

Cromsigt, J. P. G. M., H. H. T. Prins, and H. Olff. 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: Interaction of body mass and digestive strategy. *Diversity and Distributions* 15:513–522.

Does habitat selection and habitat heterogeneity facilitate coexistence of diverse grazing ungulate assemblages that differ in size? South African grazers were characterized with respect to habitat type and quality. Larger ruminant herbivores were more uniformly distributed among habitat types than smaller ones with a greater diversity of habitats used. Nonruminant grazers were more evenly distributed than ruminants, with less evidence that body size influenced the diversity or quality of habitat use.

Fryxell, J. M., J. F. Wilmshurst, A. R. E. Sinclair, D. T. Haydon, R. D. Hold, and P. A. Abrams. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecology Letters* 8:328–335.

The hypothesis that local temporal and regional spatial heterogeneity in food resources may be compensatory for species persistence is evaluated for mobile Thomson’s gazelle living under a stochastic regime of local rainfall and food availability. Model simulations parameterized with field data showed long-term persistence of Thompson’s gazelles requires adaptive, unrestricted movement over large landscapes. The spatial scale of resource heterogeneity and complex behavioral responses of grazers to spatial heterogeneity of food supplies has conservation significance.

Goheen, J. R., T. M. Palmer, G. K. Charles, et al. 2013. Piecewise disassembly of a large-herbivore community across a rainfall gradient: The UHURU experiment. *PLoS One* 8.2: e55192.

The authors present results of the “Ungulate Herbivory Under Rainfall Uncertainty” experiment to assess the abiotic context of effects of three size classes of large mammalian herbivores (LMH) on plant communities across a rainfall gradient. Excluding successively smaller-bodied subsets of the LMH community indicated that size classes are not functionally redundant in their effects on plant communities. Species-specific and context-dependent responses of plants are described.

Hempson, G. P., S. Archibald, and W. J. Bond. 2015. A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science* 350:1056–1061.

Abiotic attributes, especially temperature and precipitation, characterize global biome distributions. By reconstructing the putative form and intensity of herbivory across sub-Saharan Africa through modeling species-level biomass of ninety-two large mammalian herbivores, four ecologically distinct, continental scale herbivory regimes are recognized based on the resulting trait-based classification. Herbivory regimes, fire prevalence, soil nutrient status, and precipitation provide a continental-scale view of the role that biotic interactions from large mammalian herbivores play in determining biome distributions.

Hopcraft, J. G. C., H. Olff, and A. R. E. Sinclair. 2009. Herbivores, resources and risks: Alternating regulation along primary environmental gradients in savannas. *Trends in Ecology and Systematics* 25:119–128.

This comprehensive review synthesizes the relative contributions of abiotic features, foraging abundance and nutritional quality, body size, and predation risk for large, diverse mammalian herbivore assemblages in African savanna ecosystems. Comprehensive conceptual models and empirical trends of multiple factors illustrate how interactions among multiple factors combine and lead to both top-down and bottom-up regulation. The scale of heterogeneity determines the mode of regulation, and abiotic processes determine the direction of regulation, leading to shifting regulation along gradients of productivity.

Owen-Smith, N., D. R. Mason, and J. O. Ogutu. 2005. Correlates of survival rates for 10 African ungulate populations: Density, rainfall and predation. ***Journal of Animal Ecology*** **74:774–788.**

Seasonal, age-dependent survival of ten African ungulate species over at least fourteen years in Kruger National Park is evaluated with respect to density, rainfall, and predation to assess. In general, juvenile survival was sensitive to rainfall especially in the dry season, suggesting food limitation; adult survival decreased at high density, likely due to lion predation, with evidence for a food limitation/predation interaction.

Sensenig, R. L., M. W. Demment, and E. A. Laca. 2010. Allometric scaling predicts preferences for burned patches in a guild of Eastern African grazers. ***Ecology*** **91.10: 2898–2907.**

This study employed prescribed fires to assess the long-held belief that allometric scaling predicts smaller-bodied grazers rely on higher-quality forage than large-bodied grazers, which allows the coexistence of a diverse assemblage of herbivorous mammals in Africa through resource partitioning. Grazing locations in burned savanna by foregut fermenters had lower levels of nondigestible plant material than locations in burned savanna chosen by hindgut fermenters for grazing. Results indicate that fire-induced vegetation heterogeneity promotes resource partitioning among large herbivores.

Consumer Interactions in Food Webs

Species interactions can affect the distribution and coexistence of grazer species, either through direct use of limited resources or because of habitat modifications by one species that then affects another. Foster, et al. 2014 demonstrates that grazer impacts on non-grazing species such as birds and arthropods is body size–dependent through habitat modification roles. Piug, et al. 2001; Odadi, et al. 2011; and Ranglack, et al. 2015 investigate the role of resource availability and species interactions that modulate species coexistence in human-modified systems influenced by domestic grazers. Much emphasis on understanding species coexistence using a resource-ratio conceptual model of competitive interactions focuses on these factors, as shown in a meta-analysis on fifty-two grazing species in Murray and Baird 2008.

Foster, C. N., P. S. Barton, and D. B. Lindenmayer. 2014. Effects of native herbivores on other animals. ***Journal of Applied Ecology*** **51:929–938.**

This study includes a meta-analysis of the effect of large native grazing herbivores on other animals, showing high densities of large mammal herbivores negatively affected other animal species, mostly from changed quality or structure of vegetation. Arthropod richness responded most negatively, contrary to prior reports; abundances of birds, small mammals, and arthropods also decreased. This literature is still incomplete because of the short duration of most studies, high incidences of confounding factors, coarse metrics to assess effects, and few community-level syntheses.

Murray, M. G., and D. R. Baird. 2008. Resource-ratio theory applied to large herbivores. ***Ecology*** **89:1445–1456.**

Coexistence of up to fifty-two grazing species in the same habitat based on resource exploitation and body size is examined. The resource-ratio/resource-competition theory of ungulate communities through exploitation of plant cell wall and cell contents including positive (mineral elements) and negative attributes (chemical defenses) was used. Demand-minimizing (efficient use of limited resources) and extraction-maximizing (superior users of competitor’s most needed resources) strategies are recognized. Multispecies coexistence of grazing herbivores also depends on spatial heterogeneity.

Odadi, W. O., M. K. Karachi, S. A. Abdulrazak, and T. P. Young. 2011. African wild ungulates compete with or facilitate cattle depending on season. *Science* 333:1753–1755.

Wild ungulate competition with cattle is assessed. Cattle performance was negatively affected in the dry season through reduced food intake, a pattern reversed in the wet season, especially in response to medium-sized herbivores. Facilitation in the wet season led to increased dietary crude protein and increased ratio of digestible organic matter/crude protein in forage. Competition versus facilitation varied spatially and temporally in response to the proportion of dry and wet periods, herbivore densities, and ecosystem productivity.

Piug, S., F. Videla, M. I. Cona, and S. A. Monge. 2001. Use of food availability by guanacos (*Lama guanicoe*) and livestock in Northern Patagonia (Mendoza, Argentina). *Journal of Arid Environments* 47:291–308.

An analysis of dietary overlap in domestic and wild ungulates revealed similarity in essential food resources in a shrubby steppe environment in Argentina. The high dietary diversity of guanaco, a South American camelid, allowed this species to have less dietary competition with cattle, but other ungulates in the system, that is, goats, horses, and sheep, exhibited high habitat-specific vulnerability to shared use of food with cattle.

Ranglack, D. H., S. Durham, and J. T. du Toit. 2015. Competition on the range: Science vs. perception in a bison-cattle conflict in the western USA. *Journal of Applied Ecology* 52:467–474.

In managed grazing systems, claims of competition between livestock and wild ungulates are common. Relative grazing impacts of cattle, bison, and lagomorphs (mostly jack rabbits) in Utah are estimated in partial (bison and cattle) and full (all three species) grazing exclosures plus paired open reference plots. Lagomorphs consumed 34 percent, bison 13.7 percent, and cattle 52.3 percent of total biomass removed from shared range. In surveys, ranchers perceived bison as high-level competitors, but lagomorphs were not considered important.

Grazing Lawns

Grazing lawns are a distinct vegetation type that occur in some grasslands and savannas, characterized by short-statured grass species of high nutritional quality that persist because of grazing activity as posited in McNaughton 1984 and later elaborated upon in a more recent review, Hempson, et al. 2015. While grazing lawns have low biomass, they are often critical resources to grazers because of their high nutritive value as demonstrated in Verweij, et al. 2006, and because they are easily grazed due to the absence of low nutritional value stems that retard feeding. As long as there are sufficient soil nutrients and rainfall, foliar protein concentration is high in regrowth following foraging. Archibald 2008; Bonnet, et al. 2010; and Veldhuis, et al. 2014 describe multiple alternate hypotheses to explain the establishment and maintenance of grazing lawns, and while a full understanding of grazing lawns is not completely resolved, there is broad agreement about their importance to grazers.

Archibald, S. 2008. African grazing lawns—how fire, rainfall, and grazer numbers interact to affect grass community states. *Journal Wildlife Management* 72:492–501.

A simulation model that tests the conditions required for the initiation and spread of grazing lawns indicates lawns proliferate during periods of low rainfall, in areas characterized by infrequent fires, homogeneous soil substrate, and high grazer densities. Using the same model in a real savanna in Southern Africa demonstrated that lowering fire frequency and increases in grazer density will double the proportions of grazing lawns in the park.

Bonnet, O., H. Fritz, J. Gignoux, and M. Meuret. 2010. Challenges of foraging on a high-quality but unpredictable food source: The dynamics of grass production and consumption in savanna grazing lawns. *Journal of Ecology* 98:908–916.

This study investigates how production and consumption on grazing lawns is synchronized to provide adequate nutrition to grazers in a South African savanna during wet and dry seasons. Short-term primary productivity was strongly, positively correlated to short-term total grazing activity suggesting close synchronization, but poorly correlated to standing biomass. A threshold response by primary productivity to short-term precipitation added a stochastic element to the ability of herbivores to predict whether grazing lawns are a reliable source of forage.

Hempson, G. P., S. Archibald, W. J. Bond, et al. 2015. Ecology of grazing lawns in Africa. *Biological Reviews* 90:979–994.

This review analyzes the establishment and maintenance of grazing lawns in Africa. The interplay between rainfall, soil nutrient status, grazer community composition, and fire regime contribute to both processes. A conceptual model summarizes key interactions in the context of a precipitation gradient. Factors that concentrate grazers (e.g., nutrient hot spots and soils with high sodium reflecting underlying bedrock) determine where lawns establish. Different grazer species vary in effects on grazing lawn dynamics and the ability to feed on short-statured vegetation.

McNaughton, S. J. 1984. Grazing lawns: Animals in herds, plant form, and coevolution. *American Naturalist* 124:863–886.

This seminal works suggests gregariousness in herding animals may not only be a function of predator vigilance but also promotes reliability of foraging areas in efforts to optimize the intake of high-quality forage.

Veldhuis, M. P., R. A. Howison, R. W. Fokkema, E. Teilens, and H. Olff. 2014. A novel mechanism for grazing lawn formation: Large herbivore induced modification of the plant-soil water balance. *Journal of Ecology* 102:1506–1517.

Herbivores may affect the formation and maintenance of grazing lawns through plant–soil water balance. In a conceptual treatment, authors examine how large herbivores change the soil water balance in grazing lawns through defoliation and soil compaction, leading to shifts in the taxonomic composition of plant communities favoring drought-tolerant traits. Combined effects of defoliation and compaction led to lower soil moisture in grazing lawns because of increased soil temperatures, potential evapotranspiration rates, increased soil bulk density, and water infiltration rates.

Verweij, R. J. T., J. Verrelst, P. E. Loth, I. M. A. Heitkonig, and A. M. H. Brunsting. 2006. Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. *Oikos* 114:108–116.

High nutritional quality in forage on grazing lawns created by large herbivores during the wet season provides a critical resource for mesoherbivores. The contribution of hippopotamus and coexisting kob grazing lawns, and nearby ungrazed swards on kob performance in Cameroon is described. Hippo grazing lawns are more nutritious than both kob lawns and ungrazed swards, and meet kob energy and nutritional needs to early dry season. Kob grazing lawns do not provide subsistence nutrition, and ungrazed swards are the least profitable.

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