metamorphosis in a suitable adult habitat. For this to be possible, they need uncluttered space, either bare rock or a surface covered by a biofilm of unicellular and extra-cellular organic material. Where the surface is already covered by algae, it is impossible for the sessile species to become established. Even if larvae can settle and meta-morphose, they are usually smothered by the algae growing over them, preventing them from growing or feeding.

The grazers themselves are often eliminated by the algae once they grow large enough. Many of the inver-tebrate grazers are quite unable to consume seaweeds once they are too large. There are some invertebrates, such as sea urchins, which have no problems, but they are not usually common components of intertidal shores.

Thus, grazing by microalgal feeders frees space which is then occupied by a range of other sessile space-users and a suite of grazing species. This maintains the diversity of species from many Phyla in the assemblage. Algae grow more quickly in some areas, for example, lower on the shore, where habitats are subject to greater splash and spray during low tide and longer periods of submersion under water during high tide. As a result, in such areas, grazers are less effective and unable to keep surfaces free from foliose algae. Consequently, there are fewer animals and types of animals in such areas.

In addition to their direct consumption of plants, gra-zers, through their indirect effects on habitat, contribute a lot to the maintenance of biodiversity in assemblages of other species that are neither the food plants nor their consumers.

See also: Intermediate Disturbance Hypothesis; Optimal Foraging; Plant Defense Strategies; Plant Defense.

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Grazing Models

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Introduction
Concepts and Models

Further Reading

Introduction

Grazing Systems

A large proportion of the surface of the Earth is covered by plant communities that are grazed and browsed by livestock and/or wild herbivores. These communities include natural or seminatural grasslands and shrublands such as the veldts of South Africa, the pampas and steppes of Argentina and Uruguay, or the plains and prairies of central North America as well as man-made grasslands created by the removal of natural forests for livestock production which are common, for example, in temperate, Mediterranean, and

tropical regions (see Steppes and Prairies). Another important type of natural plant communities, which evolved with large herbivores are tropical savannas (see Savanna), that is, grasslands with scattered individual trees, which are common in Africa and Australia.

The impact of grazing and browsing animals on the dynamics and productivity of grasslands, shrublands, and savannas has been an important subject of basic and applied ecological research. Grazing is economically important because domestic livestock farming and traditional pastoral grazing systems are widespread all over the world. Here theoretical and applied questions are in mutually dependence because developing sustainable grazing management requires an understanding of the dynamics of the grazing system. Since the massive expansion of European settlers and their livestock at the beginning of the twentieth century into arid and semiarid areas of Africa, South and North America, and Australia, massive ecological changes have been observed in these rangelands. On the other hand, man maintains 'stable' grazing systems, especially in the Mediterranean, for thousands of years.

Grazing Models

Because of the complexity of the vegetation–grazer system and the long timescales of vegetation change, especially in semiarid rangelands, grazing models are an integral part of rangeland research. Conceptual models to guide management have reflected the concurrent concepts of theoretical ecology. In fact, the development of grazing models mirrored developments in theoretical ecology closely.

Early models to conceptualize grazing systems were based on equilibrium models, most notably models of ecological succession developed around 1940 (i.e., the Clementsian theory of ecological succession, Grassland Models) and predator–prey-type models developed in the 1960s. However, since the 1970s, the equilibrium paradigm of ecology (see Stability) was increasingly challenged. In the late 1980s, ecological theory became dichotomized into equilibrium and nonequilibrium camps. The first proposed that homoestatic biotic interactions (feedbacks) would cause a system to return to equilibrium after perturbation, the latter argued that environmental fluctuations and disturbances are stronger than any homoestatic biotic forces, leading to a highly stochastic system rarely at equilibrium. This dichotomy is still mirrored in the ongoing equilibrium versus nonequilibrium debate in rangeland ecology. Integral part of this debate is also the issue of spatial scale, the role of spatial heterogeneity in the plant–herbivore system.

Grazing models are as varied as the purposes for which they have been constructed, and cover various spatial and temporal scales and various degrees of detail. The objective of this article is to describe the historical development outlined above based on characteristic and influential examples of grazing models. We use the term 'grazing' in the sense of herbivory by large mammalian herbivores; this includes both grazing of herbaceous plants and browsing of woody vegetation. Reflecting the literature, we emphasize models of livestock grazing (in contrast to native game).

Concepts and Models

Equilibrium Concepts

The range succession model

The range succession model is based on the Clementsian theory of ecological succession (see Grassland Models) and formed the conceptual framework for most grazing management up to the 1980s. It supposed that a rangeland has a single persistent state (the climax) in the absence of grazing and assumes continuous and reversible transitions of the grassland state along a single, monotonic gradient between an overgrazed subclimax and an undisturbed climax state of vegetation. Therefore, the grazing pressure can be made equal and opposite to the successional tendency, producing one equilibrium in the vegetation at a set stocking rate. A sustainable yield of livestock products can be harvested from such an equilibrium (see the next section). The model supposes that both grazing and interannual rainfall variation cause vegetation changes along a continuous vegetation gradient. Therefore, the effects of a drought on vegetation can be counterbalanced by reduced grazing.

Maximizing animal gain (Jones Sandland model)

Under the assumption that vegetation responds continuously and reversibly to grazing, the fundamental question for a commercial rancher is to determine the stocking rate that maximizes the animal production per hectare. In their influential model of the mid-1970s, R. J. Jones and R. L. Sandland assumed a linear functional response of gain per animal (Y_a) to stocking rate (x), yielding a gain per hectare $Y_h(x) = ax - bx^2$, where a and b are parameters to be determined in field trials. For this model, the maximal gain per hectare occurs at stocking rate $x = a/2b$ (**Figure 1**). The functional response of gain per animal to stocking rate was widely discussed: some researchers assumed a constant gain per animal (e.g., due to metabolic limits of intake) at low stocking rates and a decreasing gain per animal beyond a critical stocking rate, due to competition among grazers. Numerous grazing trials in a wide range of grazing systems were performed to substantiate these models.
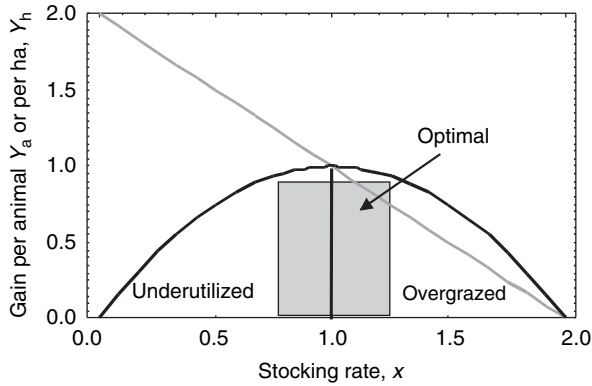
Figure 1 The Jones–Sandland model. Determination of the optimal stocking rate that maximizes the gain per hectare. Solid black line indicates gain per hectare assuming a linear decline of gain per animal with stocking rate (gray line).

Multiple Stable States

The Noy-Meir model

While most range management in the 1970s was based on the range and succession model, I. Noy-Meir analyzed plant–herbivore interactions based on predator–prey models from the 1960s (link to classical predator–prey models). He modeled the dynamics of the vegetation under grazing with a differential equation model representing grazing as a homogeneous process in space and continuous in time. His analysis produced the disturbing result that a continuously grazed ecosystem may show

dual stability. A small increase in grazing pressure or a minor disturbance may move the system from a stable state of high productivity to a stable state of low productivity. Similar system behavior had been observed at this time in other mathematical models, for example, in the famous case of the spruce budworm. The important message was that a biological resource can become suddenly overexploited by only slight increases in harvest rate and drop into a low-productivity state. Recovery is possible only after a substantial reduction of the harvest rate (i.e., hysteresis). The original Noy-Meir model has been modified in several ways (see below).

Model formulation

The Noy-Meir model, and numerous successor models, uses a general structure to describe changes in plant biomass V as

$$\mathrm{d}V/\mathrm{d}t = G(V) - C(V) \qquad [1]$$

where $G(V)$ describes plant growth as a function of plant biomass and $C(V) = H\,c(V)$ is the biomass consumed by herbivores, $c(V)$ the per capita consumption, and H the stocking rate. The simplest model of this type uses the logistic equation $G(V) = rV(1 - V/K)$ to model plant growth, and a 'Holling Type III' consumption function $C(V) = \beta H V^2/(V_0^2 + V^2)$ to model biomass loss due to consumption by herbivores. Thus, without grazing, biomass V settles at an equilibrium biomass K. The growth rate r describes how quickly V will approach the equilibrium (**Figure 2A**). The Type III consumption function
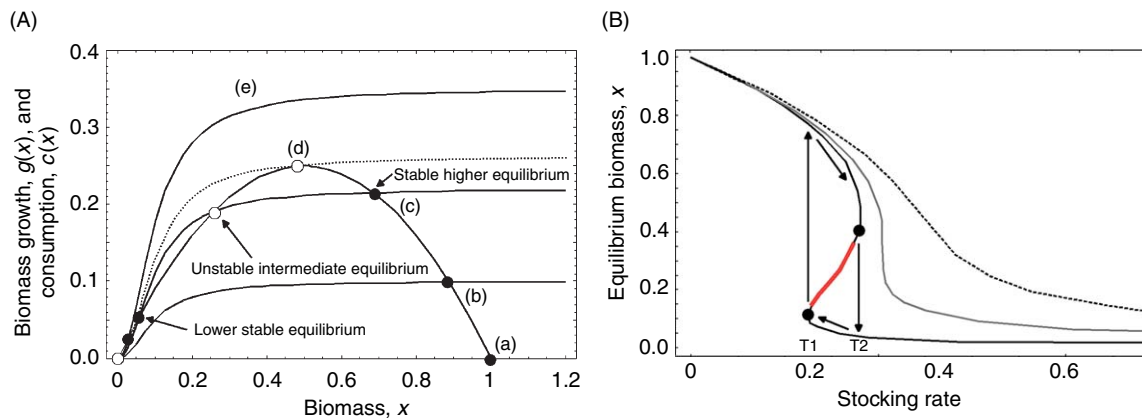

Figure 2 The Noy-Meir model. (A) The biomass growth function $g(x)$ (hump-shaped curve) and the consumption function $c(x)$ for several levels of grazing pressure (a: no grazing, b–e increasing stocking rate) versus biomass x. The parameter α selected shows multiple equilibria (i.e., $\alpha = 0.1$). Intersections are either stable (filled circles) or unstable equilibria (open circles). The dashed line shows the consumption function at the critical stocking rate $T2$. (B) The equilibrium biomass in dependence on stocking rate γ for different values of the parameter $\alpha = 0.1$ (left), 0.19 (thin gray), 0.3 (dashed line). The parameter α describes the maximum animal consumption in units of equilibrium biomass in the absence of grazing. For $\alpha = 0.1$ the curve folds and an instable equilibrium (red line) and two stable equilibria (black and gray lines) appear. If biomass is at the higher equilibrium and stocking rate exceeds the critical value $T2$, the equilibrium becomes unstable and biomass collapses rapidly to the lower equilibrium. Reducing stocking rate below $T2$, however, does not result in recovery as expected by the range succession model, but must be reduced substantially to stocking rate $T1$. This phenomenon is known as hysteresis or dual stability.

is a saturation function (**Figure 2A**): at low biomass V herbivore intake is limited by forage availability so that $C(V)$ increases with increasing biomass. However, at high biomass $C(V)$ saturates, determined by the parameter V_0, which is related to animal intake capacity or digestion rate. The resulting differential equation for biomass x yields, after rescaling, the basic form

$$dx/dt = g(x) - c(x) = x(1-x) - \gamma x^2/(\alpha^2 + x^2) \qquad [2]$$

with only two parameters $\gamma = \beta H/rK$ and $\alpha = V_0/K$. For parameter values $\alpha < 0.192$ the system shows three biological equilibria, one unstable equilibrium at intermediate biomass and two stable equilibria at low and high biomass (**Figure 2B**).

Biological interpretation

The condition $\alpha = V_0/K < 0.192$ means that the consumption function $c(x)$ saturates at a biomass x for which biomass growth $g(x)$ has not yet reached its maximum. In this case, the two functions intersect (**Figure 2A**). This general model behavior holds for modifications of $g(x)$ and $c(x)$ as long as the growth function is a convex, arch-shaped function of biomass with a single maximum and the consumption function is a saturation function of biomass which may include a residual ungrazable biomass. Noy-Meir suggested that herbivore saturation should occur at most grass–grazer systems and that dual stability should be a common phenomenon in grazing systems. However, if herbivores would be less efficient, the grazing system would show only a single stable equilibrium.

Modifications of the Noy-Meir model

Originally, the Noy-Meir model described the biomass dynamics within a single grazing season (long enough to ensure equilibrium) where grazing is a homogeneous process with constant stocking rate in space and continuous in time. However, in real grazing systems these assumptions may not apply and additional factors that influence biomass dynamics may overpower and destroy the mathematical phenomenon of dual stability. In the following we will critically review the most important modifications of the Noy-Meir model.

Bite scale

If we interpret the Noy-Meir model at the scale of a single season, grazing is not a continuous process, but involves discrete defoliation events which are followed by a variable period of regrowth. Thus, in grazed grassland, different patches will be in different states of recovery from previous defoliation events leading to a spatially heterogeneous grassland. Additionally, grazing is a stochastic process with uncertainty about the patch where animals take the next bites.

S. Schwinning and A. J. Parsons analyzed in the late 1990s the dual stability property in an extension of the Noy-Meir model describing grazing as a discrete and stochastic process at the bite scale. They found that dual stability was much less likely than previous models predicted and the potential effects of dual stability were minor because the productivities of the two stable equilibria were virtually indistinguishable in a field situation. In a second analysis, they assumed that patches with low biomass were more likely to be defoliated and found again a reduced tendency for dual stability. Instead, the system showed a tendency to generate bimodal frequency distributions (of biomass per patch) where two distinct patch populations are maintained side by side. This phenomenon has, for example, been observed repeatedly in cattle-grazed systems and is known as grazing lawns in rangelands. Further refinements of grazing models at the bite scale require a spatially explicit account of grazing within the framework of optimal foraging (see Optimal Foraging Theory).

Soil degradation

Dual stability of eqn [1] may not only be caused by the particular functional response of the grazer, but also by the shape of the vegetation growth function, which may depend on soil conditions or degradation. W. H. Schlesinger formulated at the beginning of the 1990s a conceptual model of biological feedbacks in desertification. Grazing and trampling may initiate feedback processes in water redistribution and infiltration which transform formerly homogeneous vegetation to heterogeneous vegetation distributed in patches of nutrients (islands of fertility) surrounded by a matrix of bare soil. A similar idea was followed in the end of 1990 by J. van den Koppel, M. Rietkerk, and colleagues. They developed a soil water dynamics submodel to derive a biomass growth function $G(V)$ depending on precipitation, several soil properties, and standing growth biomass V. Under the assumption that the dynamics of soil water acts on a much faster timescale than plant growth they found

$$G(V) = h \times PPT \frac{V + kW_0}{V + k} \frac{1}{uV + r_w} - l \qquad [3]$$

where PPT stands for rainfall, W_0 is the minimum water infiltration, which is reached in the absence of plants, and k, u, r_w, h, and l are site-specific constants regulating the water dynamics. The two most important parameters within this model are PPT and W_0. If the value of W_0 is low, biomass growth is a hump-shaped function of standing biomass. For example, in sparsely vegetated areas (low biomass), water is lost due to runoff and, consequently,
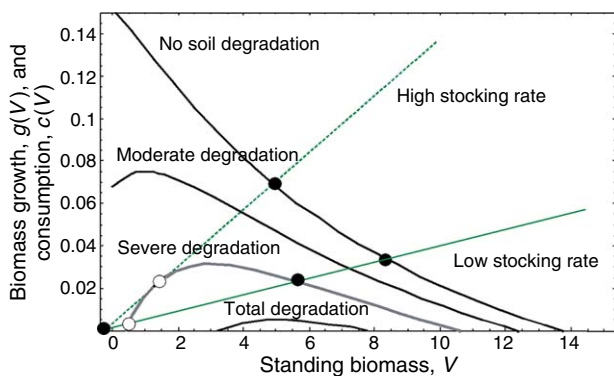
Figure 3 Multiple stable states due to soil degradation causing reduced biomass growth at small biomass values (eqn [3]). Herbivore consumption is linearly related to standing biomass (green lines). With no or moderate soil degradation, only a single stable equilibrium exists. However, under severe soil degradation growth is strongly limited at low biomass values which results in a positive feedback causing multiple stability (gray solid line). Open circles indicate unstable equilibria and filled circles stable equilibria.

biomass growth is close to zero. Biomass growth is maximal at intermediate standing biomass and decreases at high biomass due to increased competition (bold gray line in **Figure 3**). In the case of greater W_0, little water is lost due to run off. Therefore, growth is assumed to be maximal at low standing biomass and decreases thereafter due to density-dependent regulation (**Figure 3**).

Assuming a linear relation between consumption and biomass, the resulting model shows two equilibria, one at the unvegetated state and one at a vegetated state. Without soil degradation, only the vegetated state is possible (**Figure 3**) and vegetation changes are always reversible. However, irreversible vegetation shifts may occur under intermediate stocking rates and at a hump-shaped growth function assumed for degraded soils (**Figure 3**, gray solid line). The underlying mechanism for dual stability is a negative feedback between grazing and plant growth in degraded soils. If standing biomass is severely reduced due to overgrazing, plant growth cannot equilibrate consumption and the system approaches the stable unvegetated equilibrium.

Herbivore dynamics

General models of the type given in eqn [1] assume that the herbivore population is uncoupled from the dynamics of the vegetation and held at a constant density. This assumption may be reasonable for commercial ranches which buy and sell animals to keep a stocking rate; however, it does not hold, for example, in traditional pastoral grazing systems, where animal numbers are allowed to fluctuate. The simplest way to add

herbivore dynamics to the model is to assume that herbivore density changes as

$$\mathrm{d}H/\mathrm{d}t = ec(V) - d \qquad [4]$$

where d is the herbivore mortality rate and e a parameter describing the growth efficiency of the herbivore population. The resulting models are of the predator–prey type intensively studied in theoretical ecology, for example, by M. L. Rosenzweig and R. H. MacArthur, which may show stable equilibria, limit cycles, and dual stability. However, allowing for herbivore population dynamics tends to stabilize the grazing system in comparison with fixed stocking rates. This is due to the fact that deterioration of the vegetation is likely to lead to a decrease of the herbivore population size due to overexploitation of the resource. When grazing pressure is relaxed, vegetation recovers before herbivores are able to recover.

Spatially explicit herbivore dynamics on larger scales

The temporal dynamics of interacting consumer and resource populations is one of the most thoroughly studied problems of theoretical population biology (see Prey–Predator Models); however, making these models spatially explicit may alter their behavior substantially. One revealing example was given in a study of A. Basset, D. DeAngelis, and J. Diffendorfer published in 1997. They studied classical herbivore dynamics similar to eqns [1] and [4], but implemented it on a spatially explicit grid. The vegetation dynamics within each grid cell was described by logistic growth, but the grazers could move across the landscape of patchily distributed grass resources to neighboring cells. The grazer had less than perfect information concerning the grass biomass in other patches leaving a cell out if the expected intake became too low. The herbivore consumption rate was modeled using the functional responses $C(V) \sim V^n/(V_0 + V^n)$ which yields for $n = 1$ the Holling type II response (herbivore saturation and efficient grazer at low biomass), and for $n = 2$ a Holling type III response (less-efficient grazer, biomass protected at low densities).

Basset and co-authors selected parameter values based on the behavior of the nonspatial model. With efficient grazers ($n = 1$), herbivore–vegetation dynamics was unstable, producing propagating oscillations, while less-efficient grazers ($n = 2$ or $n = 3$) stabilized the system. Simulations of the corresponding spatially explicit system indicated a reversal of the relationship between functional response and stability. The underlying mechanism of this finding is that an efficient grazer completely exploits the patch before leaving it. However, because the grazer has no global knowledge on the distribution of grass biomass on the entire landscape, there are always patches that escape from grazing for a period of time that is long enough to recover. This is one hypothesis explaining the

long-term stability of natural grazing systems where huge herds of wild herbivores once roamed over the prairies of the US or the savannas of Africa. The question of large-scale herd movement is also of importance in grazing systems where substantial temporal variation in food resources occurs over time. In this case, local food scarceness can be compensated by movement of large herds to take advantage of ephemeral spatial distribution of food resources. Species of high conservation interest with herd movements are, for example, Thomson's gazelles living on the Serengeti Plains, East Africa, Saiga antelopes in Kalmykia, Mongolian gazelles, or reindeer in the Taymyr in the Russian Arctic.

Spatial pattern formation

The assumption of spatial homogeneity does not apply in many grazing systems, especially in arid and semiarid environments. If average rainfall is too low to allow for a continuous vegetation cover, vegetation will typically show a patchy distribution with a matrix of bare soil interspersed with vegetated patches. On degraded soils, a negative feedback between grazing and plant growth causes two equilibria, one of bare soil and a vegetated state (**Figure 3**). Given that these two states may coexist spatially side by side, this process would explain the frequently observed spatial pattern of a two-phase mosaic, where vegetated patches are interspersed into a matrix of bare soil (see Ecosystem Patterns and Processes). This idea was tested in several modeling studies that explored spatially explicit or implicit modifications of the nonspatial models based on eqn [3]. These models were successful in reproducing patterns similar to the observed ones. This result is a first step toward showing the validity of the underlying hypothesis. However, it is well known that models based on substantially different mechanisms or processes may reproduce the same pattern. Thus, more rigorous comparisons between nature and models will be needed to test the validity of the hypothesis modeled.

Environmental variability

Environmental conditions, such as temperature or precipitation, are important drivers of plant growth and are not temporally constant in real systems. For example, in many arid and semiarid systems, precipitation is highly variable and unpredictable. Additionally, there is often an autocorrelation in rainfall which produces prolonged wet and dry periods at timescales of decades. To appropriately investigate the effect of grazing in such systems the stochastic rainfall needs to be considered explicitly. To date, the grazing models presented above failed to account for this inherent characteristic of semiarid and arid grazing systems and are thus restricted to, for example, temperate systems as in middle Europe, where environmental stochasticity plays a minor role for resource dynamics. It is intuitively clear that strong rainfall stochasticity will destroy the filigree structure of the deterministic models. The degree of stochasticity of environmental fluctuations, at which stochasticity dominates the behavior of the system, is yet to be determined.

Equilibrium versus Nonequilibrium Concepts

General ecological theory

At the end of the 1980s, the equilibrium view of ecological systems seemed unsatisfactory to a large fraction of ecologists. Most notably, in 1987, D. L. DeAngelis and J. C. Waterhouse developed a general theoretical framework for equilibrium-related concepts that includes both equilibrium and nonequilibrium behavior of ecosystems (see Stability). DeAngelis and Waterhouse point out that the (non)equilibrium behavior of an ecosystem may depend on spatial scale. For example, systems that are unstable at small spatial scales (e.g., paddock scale) may be stable on the landscape scale. This is illustrated above by the example of the grazer–vegetation system in the section titled 'Spatially explicit herbivore dynamics on larger scales'. Metapopulations are another important example for ecological systems that are stochastically dominated at the local patch scale but may show equilibrium at the landscape scale. Finally, hierarchical patch dynamics is a paradigm to describe interacting, equilibrium and nonequilibrium, dynamics at multiple spatial and temporal scales.

The equilibrium versus nonequilibrium debate in rangeland ecology

These advances in general theory were mirrored in rangeland science. One year after the review by DeAngelis and Waterhouse, J. E. Ellis and D. M. Swift published an influential paper on East African pastoral ecosystems which stimulated an ardent debate about equilibrium versus nonequilibrium concepts in arid and semiarid grazing systems. They showed evidence for nonequilibrium dynamics of a pastoralist ecosystem and argued that a fundamental misunderstanding of the ecological dynamics based on equilibrium concepts may lead to inappropriate and failed interventions. The emerging 'new rangeland ecology' posits that traditional, equilibrium-based rangeland models have not taken into account the considerable spatiotemporal heterogeneity and climatic variability of semiarid rangelands, and that mobility, variable stocking rates, and adaptive management are essential for effectively and sustainably utilizing semiarid and arid rangelands.

Central to the debate became the question about the relative importance of biotic and abiotic factors in driving rangeland production. This includes the question if, and how, grazing may affect vegetation dynamics, and if

grazing may induce rangeland degradation. This has led to concerns about the ecological consequences of uncritically adopting the nonequilibrium paradigm for management in areas which are not predominantly experiencing nonequilibrium dynamics. The debate also gained heat because of confusion regarding spatial and temporal scales: One problem difficult to overcome is the mismatch between the scales of ecological investigation and those at which ecological processes take place. Since rangeland degradation usually takes place over timescales much greater than those at which management decisions are made, degradation may not be appropriately perceived. An additional problem is that the question of the relative importance of herbivores and stochastic rainfall for vegetation dynamics cannot be answered in general, but only for specific systems based on the biological information on hand and for well-defined spatial and temporal scales. The debate expanded from its initial focus on communal rangelands in sub-Saharan Africa to other continents and tenure systems, such as commercial rangelands in Australia and pastoral regions of Asia.

Models Not Relying on the Equilibrium Concept

Specific properties make the dynamics of arid and semi-arid communities difficult to analyze, including long life-spans of dominant plants, and episodic and event-driven changes in species composition occurring on long timescales in response to rare or extreme (rainfall) events. Because of these characteristics, a deeper analysis of these systems requires models which are able to include specific biological information about life-history traits of individual species and to specify the stochastic character of driving events. Theoretical top-down models which are generally not linked to specific spatial and temporal scales are unsuitable for this purpose. Instead, the development of powerful computers facilitated a new approach of bottom-up modeling.

Grid-, rule-, and individual-based simulation models

Although there is little (long-term) field data available on the full dynamics of arid plant communities, attributes of individual plant behavior such as conditions for seed production, recruitment, or mortality are relatively easy to observe at smaller temporal and spatial scales. The basic idea is therefore to incorporate the short-term knowledge in the form of rules or simple mathematical equations into a computer simulation model. In order to investigate community dynamics, these models use external drivers such as rainfall and simulate fate and interactions of individual plants within the community. This way, these models extrapolate from the behavior of individual plants to long-term community dynamics.

The Karoo model

One early example of this approach is a model developed in the mid-1990s by T. Wiegand, S. J. Milton, and colleagues describing the community dynamics of a shrub community in the semiarid Karoo, South Africa (**Figure 4**). The model is based on detailed life-history data for the five dominant species and on monthly long-term rainfall data for this region. Growth, death, seed production, germination, and seedling establishment of individual shrubs are modeled over long timescales in monthly time-steps under the influence of the stochastic and unpredictable rainfall. Observed spatial relationships, for example, on establishment, are used as rules (**Figure 4b**), instead of attempting to model them on a detailed mechanistic basis. This is an important feature of this model type, making models simple but structurally realistic.

The model shows that the dynamics of the ungrazed shrub community are typified by episodic and discontinuous changes in species composition with intervening quasi-stable phases lasting some decades (**Figures 5a and 5b**). The reason for this episodic behavior is that rainfall allows for recruitment only in a few years (**Figure 5b**) and sufficient space must be available to create low-competition sites for recruitment. Reduced seed production due to sheep grazing reduces the potential of palatable species to recruit and causes substantial changes in species composition toward unpalatable species (**Figure 5b**). Once a long-lived cohort of unpalatable shrubs is established, low-competition sites become rare and palatable species cannot respond to favorable rain sequences with recruitment, even if grazing pressure is relaxed. Therefore, rehabilitation after overgrazing may last several decades until cohorts of unpalatable shrubs die.

The rule-based approach is quite flexible and can also be extended to situations where different life forms occur at different scales. Examples are a model developed by F. Jeltsch and colleagues on the Savanna dynamics and bush encroachment in the semiarid Kalahari. In this model, space is represented as a grid of cells 5 m × 5 m in size. Each cell contains information on the life-form classes locally present (trees, shrubs, perennial gasses and herbs, annuals). In an annual time step, the spatial vegetation changes in response to rainfall, interactions among vegetation in different cells, and to grazing and fire. In a series of analyses, the model was used to investigate the coexistence of woody and grassy plants, and to study scenarios of increased shrub encroachment (at the expense of grassy vegetation) due to grazing.

In the 2000s F. D. Richardson and colleagues analyzed a detailed model that simulated a semiarid shrubland
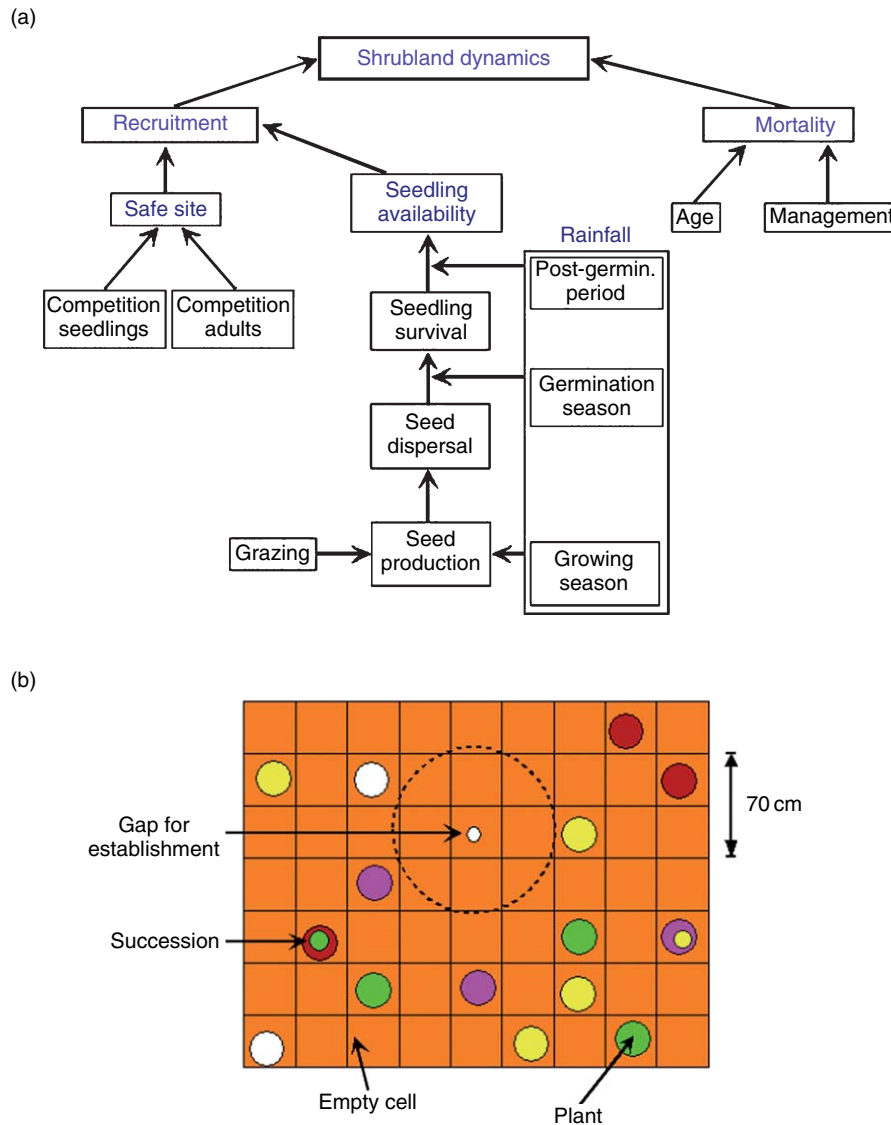
(a)

(b)

Figure 4   Grid- and rule- and individual-based simulation model, exemplified by the Karoo model. Here the main influence of grazing is modeled as reduced seed production as sheep feed on the flowers of palatable species. (a) Process chart for the fate of individual shrubs; (b) Influence of space on the fate of individual plants. The different colors indicate different species.

pastoral system of a Namaqualand communal rangeland in South Africa, including sheep and goat grazing. They found complex dynamics, for example, one single model run displayed equilibrium, disequilibrium, and threshold behavior.

Process-based models
Process-based ecosystem models (see Ecosystem Ecology) which describe plant growth, soil water, or carbon fluxes have a long tradition, especially in grassland modeling. However, their utility has been often hampered by the inability to provide a spatial distribution of the

complete set of required model parameters and initial conditions. The availability of remote-sensing data may probably close this gap. The utility of this approach was demonstrated in a study by Y. Nouvellon in the 2000s who coupled a grassland ecosystem model for semiarid perennial grasslands in southeastern Arizona (USA) with Landsat imagery data for a 10-year simulation of carbon and water budgets.

Landscape-scale models
The individual-based approach described above in the Karoo model is well suited for modeling a small plot of
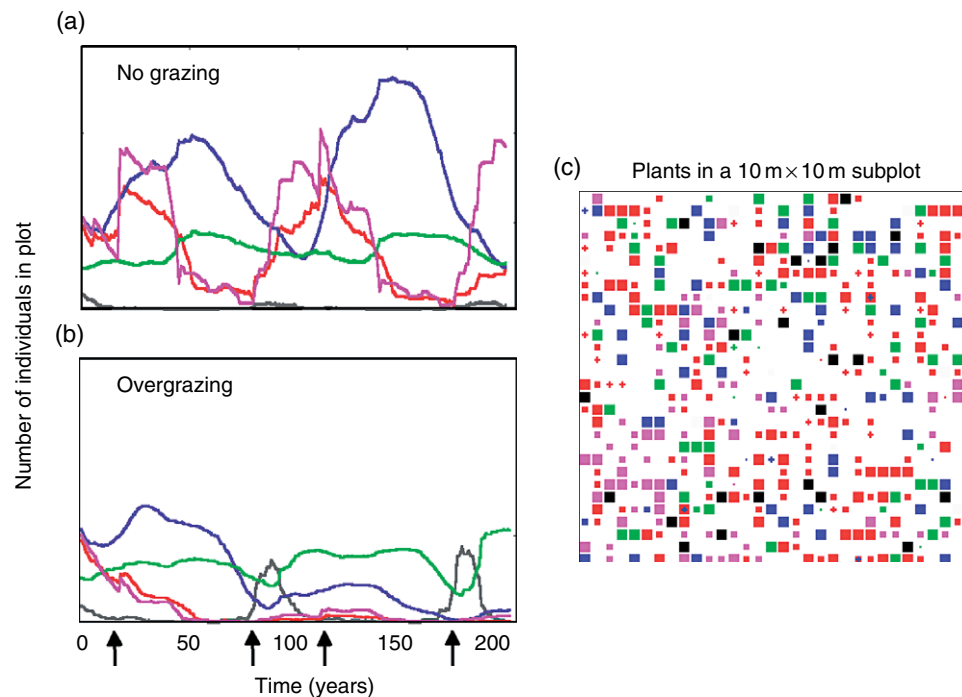
(a)

Figure 5 Karoo model. Output of a simulation using long-term rainfall from the study site. (a) A 200-year simulation without grazing showing episodic and event-driven behavior but coexistence of the five dominant species. (b) Same rainfall sequence as in (a), but reduced seed production of palatable species (blue and red). The palatable species go extinct because seed limitation produces failure to respond to favorable events (arrows). However, because of long life-span, substantial changes in species composition become only apparent several decades after initiation of grazing. (c) Snapshot of a 10 m × 10 m representative area of the simulation plot in good condition. The colours in (a), (b), and (c) represent the different species.

vegetation. This is sufficient if the aim is to identify the basic dynamic behavior and the driving demographic events in the system. However, a number of applied questions related to grazing require consideration of the landscape scale to accommodate environmental heterogeneity and paddocks, ranch, or even larger scales.

Upscaling individual-based models

In a hierarchical system without strong coupling between hierarchical levels, most detail occurring at the small scale would even out when the system is viewed from the next higher level. In this case, there would be no need to upscale an individual-based level because different factors would determine the dynamics at different hierarchical levels. However, herbivore behavior, and feedbacks between the spatial structure of the vegetation, grazing, and local water distribution affect individual plants at a smaller scale, while resulting degradation is perceived only at a larger scales. If such coupling between hierarchical levels is probable, an upscaling of small-scale models into a landscape scale is required to transport the essential information from the smaller scale to the larger scale.

In such an upscaled model, the entire plot of the original model, for example, covering a 30 m × 30 m area, may become a grid cell of the larger-scale landscape model and rules describing the spatial interactions of the landscape cells need to be defined. To model real landscapes, remote-sensing data may be used to define the environmental parameters and the vegetation of the grid cells. Since remote-sensing data are continuously collected for more than 20 years now, time-series data of plots with known climatic and management history can be used to indirectly adjust parameters and processes of the upscaled model.

Landscape scale models using remote sensing

If cross-scale coupling is weak, one approach to assess grazing effects on a landscape scale is to use animal distribution models, for example, by treating animal movement as a single pulse emanating from a waterpoint and spreading across the landscape, and to calibrate them with measured changes in vegetation cover through time and over large areas with data collected by remote-sensing satellites. This approach was developed in the 1990s by G. Pickup for arid landscapes in Australia.

Models including ecological and economic factors

Since the mid-1990s, it has been increasingly recognized that grazing systems are not only a matter of vegetation and herbivores, but are tightly embedded into the social and economic system. Even if a rancher or a pastoralist would have knowledge of the full dynamical features of his grazing system, socioeconomic factors or governmental regulations may force him not to adopt the ecologically optimal management strategy. Simulation modeling is ideally suited to solve conflicts between resource conservation and economic production because extensive simulation experiments, analyzed within the framework of ecological economics, allow for testing a broad range of management strategies and facilitate a systematic search for optimal strategies which balance between resource conservation and economic production. Here, risk assessment and multicriteria decision analysis are required to deal with the considerable uncertainty imposed by environmental and economic factors.

See also: Alpine Ecosystems and the High-Elevation Treeline; Ecosystem Ecology; Ecosystem Patterns and Processes; Grassland Models; Optimal Foraging Theory; Prey–Predator Models; Savanna; Stability.

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Greenhouses, Microcosms, and Mesocosms

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Introduction	Case Study: Coral Reef Microcosm
Physical/Chemical Control Parameters	Case Study: Florida Everglades Mesocosm
Biotic Parameters	Case Study: Biosphere 2
The Operational Imperative	Further Reading

Introduction

An ecosystem is an assemblage of organisms living together and interacting with each other and their environment. An element of biodiversity and biogeochemical time stability is implied, although dimensions are optional, ranging from the biosphere subset, the biome, to perhaps a field or pond. Ecosystems with their complex food webs and biotic physical/chemical relationships are self-organizing due to the genetic information existing in