
Generation and Maintenance of Heterogeneity in the Serengeti Ecosystem

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An observer can gaze across the Serengeti grasslands and view a veritable sea of red oat grass (*Themeda triandra*), broken only by rolling hills and the occasional solitary *Acacia*. An unknowing spectator might assume the *Themeda*-dominated grassland represents a homogeneous community type, lacking complexity, and providing constant vegetation biomass to hungry, wandering ungulates. Likewise, in the northern woodlands, one may view seemingly uniform *Acacia*- or *Terminalia*-dominated woodland and assume a similar lack of complexity. While the grasslands and woodlands of Serengeti may give the illusion of modest variation, our observer would be incorrect to assume that the ecosystem is composed of different habitats (i.e., grassland and woodland) that are themselves homogeneous. Although heterogeneity has been acknowledged as a fundamental and conspicuous feature of other savanna ecosystems (Scholes 1990; du Toit, Rogers, and Biggs 2003), vegetation, soil, and landscape heterogeneity of the Serengeti has been largely overlooked because of its abundance of herbivore and carnivore species.

The purpose of this chapter is to describe the abiotic (e.g., soils, climate, landscape) and biotic (e.g., plant, animal) patterns of heterogeneity in Serengeti and identify processes that contribute to their generation and maintenance. In this chapter, patterns of heterogeneity in Serengeti are described in terms of the nature of their measurement—whether qualitative or quantitative—and the extent to which they included a spatial component. Furthermore, we identify how humans have impacted natural

patterns of heterogeneity across the Serengeti ecosystem within the last century. Moreover, because abiotic and biotic sources of heterogeneity can interact in complex ways and can produce unpredictable results, we conclude the chapter by discussing three examples of heterogeneity generated and maintained by complex interactions between abiotic and biotic sources. Although we review processes germane to a wide range of organisms, much of the chapter deals with heterogeneity of soils and vegetation, because the majority of data on Serengeti heterogeneity are confined to those topics. While we acknowledge the importance of temporal heterogeneity, the chapter largely focuses on spatial heterogeneity, again because of data limitations. In this chapter, the Serengeti-Mara ecosystem will be collectively referred to as Serengeti. The Serengeti (see fig. 2.1) thus describes the national park in Tanzania, the Maasai-Mara National Reserve in Kenya, and the network of surrounding game reserves used by the wildebeest during their annual migration (Thirgood et al. 2004).

CONCEPTUAL ISSUES

Defining Heterogeneity

There is a vast technical and theoretical literature on concepts associated with heterogeneity, variation, and scale (Kolasa and Pickett 1991; Turner and Gardner 1991; Peterson and Parker 1998; Hutchings, Wijesinghe, and John 2000; Pickett, Cadenasso, and Benning 2003), and, except for a brief review of major concepts, the conclusions will not be reiterated here. Heterogeneity describes the degree to which elements or constituents of a system are different. This differs from variation, which describes different values of a variable of one kind (Kolasa and Rollo 1991). Under these definitions, differences in tree species composition represents heterogeneity, differences in total soil nitrogen represents variation. However, these terms, meant to make tractable a complex subject (Kolasa and Rollo 1991), may oversimplify the concepts.

In an attempt to quell the confusion associated with the terminology used to describe heterogeneity, Li and Reynolds (1995) and Weins (2000) recognized different types of heterogeneity that form a gradient from spatially implicit to spatially explicit. Weins (2000) defined four types of heterogeneity: spatial variance, patterned variance, compositional variance, and locational variance (box 5.1). These terms will be used in the following pages because they provide a framework for understanding how heterogeneity is measured and they allow an organized presentation of different types of heterogeneity as it applies to Serengeti. *Spatial variance* describes

the simple statistical measure of dispersion associated with quantitative samples collected from different locations within a given area. This type of variance lacks explicit spatial information; the average deviation from the mean is indicated without reference to where samples occurred in space. *Patterned variance* is also a measure of dispersion among quantitative samples, but it incorporates a spatial reference. Patterned variance is still not spatially explicit, but it contains information about average differences among samples in relation to their proximity, that is, conveying that samples nearby one another tend to be similar, or patches of a particular size tend to be regularly spaced across a landscape. Spatial and patterned variance measure heterogeneity of quantitative data, but properties of a system can also vary qualitatively, such as when samples contain different species, vegetation, or soil types. *Compositional variance* describes qualitative differences among samples, but like spatial variance, does not contain spatial information regarding samples. Instead, compositional variance describes average qualitative properties of a system, such as association, dissociation, patchiness, or nestedness. Finally, *locational variance* describes qualitative differences among samples in which the spatial relations among all samples are explicit.

A final conceptual point requires clarification, and that is to differentiate between processes that generate heterogeneity and organisms that respond to heterogeneity. For example, variation in vegetation height, biomass, or composition may represent a significant source of heterogeneity for organisms in a community. However, in addition to being a source of heterogeneity, plants themselves respond to heterogeneity in climate, landscape, soil, or topographic variation. In a conceptual framework of heterogeneity (Pickett, Cadenasso, and Jones 2000; Pickett, Cadenasso, and Benning 2003), processes that generate heterogeneity are represented as chains that are linked through a series of interactions: agents → substrate → *heterogeneity* → recipient → *response*. Active components are underlined and those components that respond are in italics. Agents generate, modify, or sustain functional or structural properties of a system (Pickett, Cadenasso, and Benning 2003). We will use this term to refer to processes that generate heterogeneity; later in the chapter we will distinguish between biotic and abiotic agents. The substrate is the physical entity on which agents act, but it need not be inanimate; a grassland sward is the substrate for a herd of foraging Cape buffalo. Conditions not shown in the chain, called *controllers* (Pickett, Cadenasso and Benning, 2003), can change the effect of an agent on a substrate. For example, the density of animals, water content of the soil, or time since previous defoliation will all change the effect that buffalo have on creating heterogeneity in the grassland sward. Finally, heterogene-

Box 5.1. Glossary of terms used in this chapter

TYPES OF HETEROGENEITY (FROM WEINS 2000)

Spatial variance—The simple statistical measure of dispersion associated with quantitative samples collected from different locations within a given area. Typical measures include variance, coefficient of variation, or variance/mean ratio.

Patterned variance—A measure of statistical dispersion among quantitative samples that contains information about average differences between samples in relation to their spatial proximity. Typical measurements include mean patch size, fractal dimension, lacuarity, correlograms, and semivariance.

Compositional variance—Describes qualitative differences between samples without including spatial information. Typical measurements are % similarity, evenness, patchiness index, and β -diversity.

Locational variance—Describes qualitative differences among samples in which the spatial relations among all samples are explicit. Typical measurements include mean nearest-neighbor distance, wavelet variance, and the proximity index.

Measures of Heterogeneity Used in This Chapter

Variance (s^2 or σ^2)—A statistical measure of dispersion among values in a population or a sample equal to the average squared deviation of values from the mean.

Coefficient of variance (CV)—A statistical measure of spatial variance used to compare data sets with different means. $CV = (\text{standard deviation/mean}) \times 100$.

Fractal dimension (D)—Also known as the Hausdorff Dimension, it is the power ($0 < D < 3$) used to describe the space-filling properties of lines, surfaces, and volumes. In the case of Euclidean objects such as straight lines, squares, and cubes, $D =$ an integer value (1, 2, and 3, respectively), while with fractal objects D is a noninteger value.

Semivariance (γ)—An autocorrelation statistic that estimates patterned variance by measuring the variance among samples as a function of the distance between them (h). Semivariance as a function of distance is: $\gamma(h) = [1/2 N(h)] \Sigma (z_i - z_{i+h})^2$; where $N(h)$ is the number of samples pairs used to calculate γ at distance class h , z_i is the measured value at point i , and z_{i+h} is the measured value at point $i + h$.

Beta-diversity (β)—A measure of among-sample species' compositional

variance. In this chapter, $\beta = 1 - PS$, where PS is the % compositional similarity between plots. It should be noted that there are many ways of calculating β , and many theoretical issues associated with its estimation (see Velland 2001 for a discussion).

Heterogeneity As a Process

Agents—Abiotic or biotic processes that generate and maintain heterogeneity.

Substrates—The physical entities on which agents act.

Recipients—The organisms that perceive heterogeneity and in which there is elicited a response.

ity that is induced in the substrate is recognized by a recipient organism, in which there is elicited some response. So that there is a clear distinction between the sources that generate heterogeneity, the physical entities that display heterogeneity, and the organisms that respond to heterogeneity, we make the distinction among agents, substrates, and recipients throughout the chapter (box 5.1).

Heterogeneity across Scales

Different types of heterogeneity are relevant to different organisms (recipients) at different spatial and temporal scales. Natural processes themselves do not have a single scale at which they act, but rather the scale is defined by a recipient analyzing information at a given scale (McNaughton 1989; Allen and Hoekstra 1991). The scale at which organisms perceive resources, disturbances, threats, and so on, in their environment is proportional to their body size. Therefore, the importance of a particular agent in generating heterogeneity within a community is mediated by the body sizes of the recipients inhabiting it. In Serengeti, those processes range from deposition of urine and dung at small scales to gradients of climate and geomorphology at large scales.

On the temporal axis of fig 5.1, the position of an agent is determined by the relative amount of time its action persists on a substrate. For example, a termite colony and feeding ungulate exert influence on vegetation at similar spatial scales, a few square meters, but termites have effects on the physical and chemical properties of soil that can be long lasting (Jouquet et al.

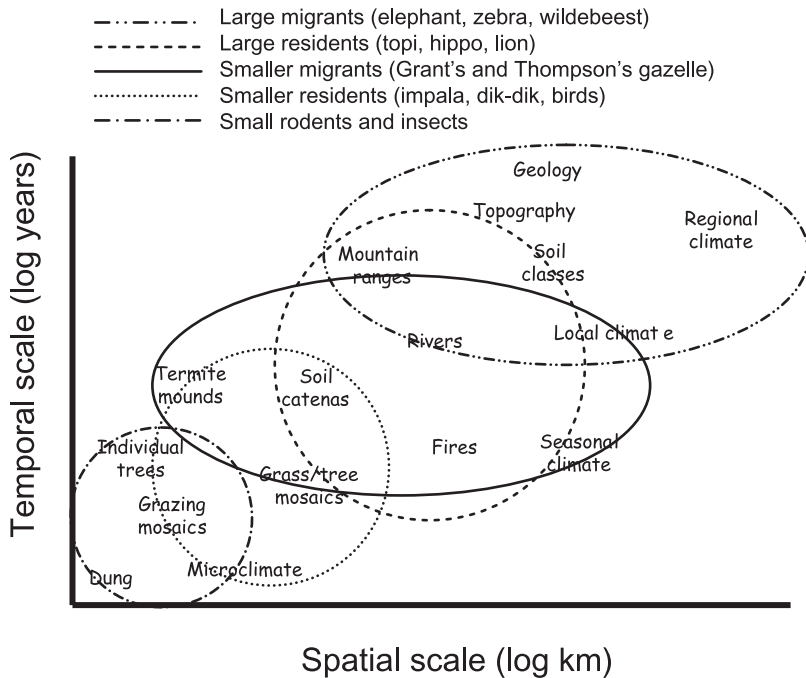


Fig. 5.1 A schematic depicting the major agents of heterogeneity in the Serengeti ecosystem, plotted as a function of the temporal and spatial scale at which they have their primary influence. The temporal and spatial scales over which different organisms are primarily influenced are represented as circles and ellipses. Migratory species have elliptical regions of influence (wide on the spatial axis) because they encounter a much greater habitat area than resident species. The agents that overlap species regions of influence are hypothesized to be those most important in the generation of heterogeneity for those species.

2002), while the impact of defoliation can vanish within just a few months (Oesterheld and McNaughton 1988). The radius of influence of individual trees in savannas is between 4 and 12 m for a mature tree (Belsky et al. 1989), while fires can consume huge grassland swards (Stocks et al. 1996). Yet the effects of trees can be long lasting: *Acacia tortilis* can live more than 100 yr (Prins and van der Jeugd 1993), compared to the effects of fire, which can disappear after just 3 months (van de Vijver, Poot, and Prins 1999).

PATTERNS OF HETEROGENEITY IN SERENGETI

Across the Serengeti's gradient of soil fertility and rainfall, there are significant changes in woody vegetation (Herlocker 1976; Norton-Griffiths 1979) and grassland cover, composition, and structure (McNaughton 1983, 1985).

Dominant grasses change across the Serengeti plains, from short to intermediate, to tall from the southeast to the northwest, respectively (Anderson and Talbot 1965; Sinclair 1979). In the northern woodlands, tree height, density, and species richness increase with rainfall (Norton-Griffiths 1979; Metzger 2002). But what is the pattern of heterogeneity across the same gradient? To answer this we must first determine the best way to measure heterogeneity across Serengeti. As suggested in the previous section, the answer depends on the agents, substrates, and recipients of interest, the type of variance data collected (spatial, patterned, etc.), and scale. In the following summary, we group the available data for Serengeti based on whether they measure compositional, spatial, or patterned variance.

Compositional Variance

Two soil maps, one for the Serengeti plains (de Wit 1978) and another for the northern woodlands and western corridor (Jager 1982) revealed the complexity and heterogeneity of soil types across Serengeti (fig. 5.2, panel A). Likewise, the understanding of Serengeti landscape heterogeneity was improved tremendously by Gerreshiem's (1974) landscape classification (fig. 5.2, panel B); the map classified the Serengeti into areas of similar topography, geologic history, and climate, called Land Regions (hereafter regions). No spatially explicit statistics of association, variance, contiguity, and so forth, have ever been attempted with these maps, but current methods of landscape ecology provide a tremendous opportunity to link soil and landscape heterogeneity to the distribution and abundance of plants and animals.

In terms of herbaceous vegetation, Belsky (1988) measured among-quadrant β -diversity (box 5.1) at 16 sites, oriented north-south from the Serengeti plains to near Lobo. She concluded that plant compositional variation was greatest in the center of the national park and lower in the south and north; she had only one sample in the western corridor. Her data suggested that the presence of termite mounds and greater Na^+ availability were associated with greater β -diversity. McNaughton (1994) analyzed data collected from 103 sites (McNaughton 1983) and showed that β -diversity was greatest in the western corridor, but that it was also high in the eastern corridor and the central hills. McNaughton's analysis linked compositional variation to landscape position; β -diversity showed a unimodal response to topographic position. The results of β -diversity measured at 104 sites by Anderson (2004) largely supported the conclusions reached by Belsky (1988) and McNaughton (1983, 1994). However, a map of β -diversity across

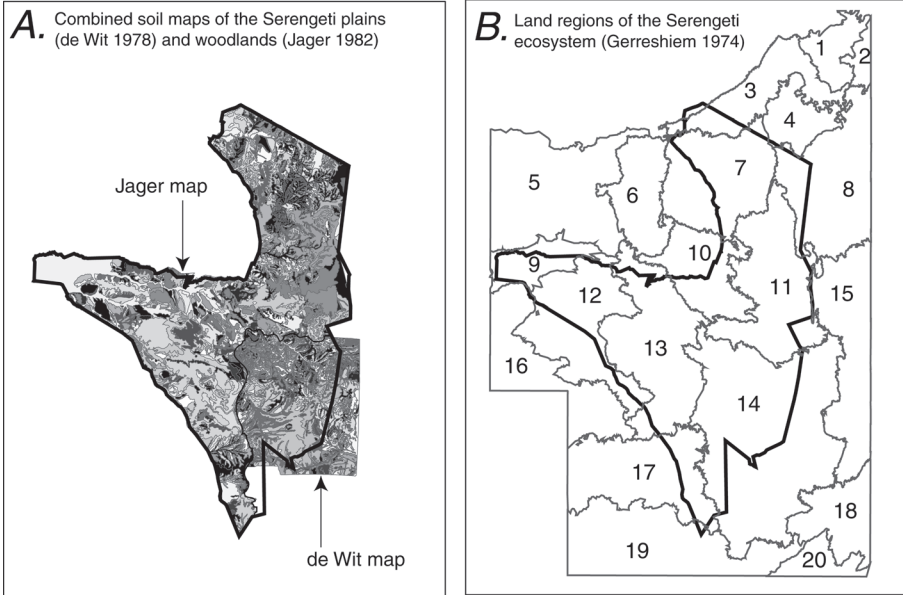


Fig. 5.2 Maps depicting patterns of compositional variance in soils and landscape features across the Serengeti ecosystem. (A) Soil maps from de Wit (1974) and Jager (1982); different shaded polygons from the Jager map (western and eastern corridor and northern extension) represent soil types grouped by soil depth, texture, and color; different shaded polygons from the de Wit map represent a hierarchical classification of soil type based on catena position, depth, texture, and geological parent type (note the finer-scale resolution of the de Wit map). (B) Serengeti Land Regions, as described by Gerreshiem (1974); Land Regions (grey lines) are main landscape types that share a common geologic history and climatic regime and have undergone comparable geomorphic influence (Gerreshiem 1974). Land Regions are themselves composed of successively smaller units called Sub-Regions, Land Systems, Land Elements, and Land Facets (not shown), which create a hierarchy of landscape classification. Smaller units in the hierarchy provide more specific information about landscape position, geologic parent material, vegetation, geologic features, and hydrology.

the Serengeti (fig. 5.3) suggests it may be an oversimplification to conclude that the greatest vegetation compositional variance exists in a band that transects the center of the Serengeti. First, high β -diversity clearly exists in the northern grasslands as well as in the central hills and the western corridor. Second, adjacent sites in the central hills and north often show great disparity in β -diversity, suggesting that within-region compositional variation may be as significant as among-region variation.

Compositional variance of woody vegetation in Serengeti was studied by Herlocker (1976) and more recently by Metzger (2002). Their studies revealed heterogeneity related to variation in topography, soil, and climate. Herlocker (1976) reported that 87.8% of the area supporting woody vegetation in Serengeti National Park was deciduous to semideciduous thorn tree

woodland, but that this vegetation type was composed of a heterogeneous mix of 38 different dominant tree species combinations (species-types) of the genera *Acacia*, *Commiphora*, and very rarely, *Lonchocarpus* (Herlocker 1976). These species-types occur in a highly reticulated pattern that mirrors topographical variation across the landscape. The second most abundant woody vegetation type (4.7%) was semideciduous woodland composed of *Combretum molle* and *Terminalia mollis*, which occurs on sandy ridge tops and upper hill slopes in a large patch (~ 400 km²) in the northwest of the park. Semideciduous thorn tree wooded grassland occupied 2.7% of the woody vegetation and is dominated by *Balanites aegyptiaca*; it occurs in a few large patches to the west of Moru kopjes and in multiple small stands near

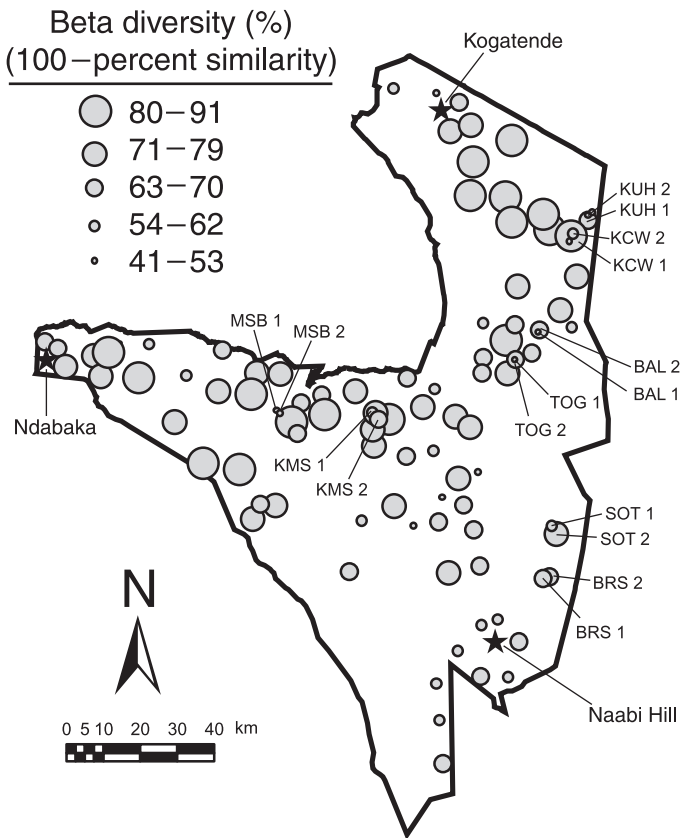


Fig. 5.3 Spatial distribution of plant species' β -diversity (measured as 100 – % similarity) in Serengeti National Park (dark line); large values of β indicate greater plant species dissimilarity among 1 m² subplots at a site ($n = 104$). Sites ($n = 8$) in which detailed sampling occurred (see text) are represented with three-letter codes; two plots were studied at each site, indicated by the number following the three-letter site code. Rain gauge locations, discussed later in the chapter, are indicated by stars.

the Grumeti River in the western corridor, and the Mara triangle. Semideciduous bushland and deciduous bushland (1.4%), composed primarily of *Acacia mellifera*, is found on bare, eroded, or disturbed soils throughout the western corridor or is associated with termite mounds in the north. At the time of Herlocker's survey, evergreen forests and evergreen to semideciduous bushland occupied 2.9% of the total woody vegetation and occurred as narrow and often discontinuous vegetation bands that paralleled the Mara, Grumeti, Orangi, and Mbalageti rivers throughout the northern extension and western corridor (Herlocker 1976). Inselberg vegetation, scattered throughout the Serengeti plains, Simiyu area and north of the Mara River, makes up a rather small (0.6%) but important part of the woody plant heterogeneity in Serengeti (see the following).

Compositional variation was also measured by Folse (1982), who studied the abundance of arthropods and birds at five sites from the Serengeti plains to the woodlands near Seronera. Arthropod abundance was greatest at the woodland site and generally decreased toward the short-grass plains. Many arthropod families showed site-dependent seasonal fluctuations in abundance, but total variation in arthropod abundance was negatively related to vegetation biomass and little variation was observed in the Serengeti plains. Bird species composition and abundance was highly variable in time and space throughout the study, but species showed significant habitat partitioning based on foraging behavior. Cursorial species required open, low-stature vegetation, while foliage-gleaners preferred dense, high-biomass vegetation. Bird species richness and abundance was greatest at sites with low vegetation height but a complex vertical structure because they could support both cursorial and foliage-gleaning feeding guilds. In general, bird densities did not track food availability (i.e., arthropods), but instead were correlated with vegetation greenness, which has a strong seasonal component and depends on the periodicity of local rain events.

Spatial Variance

We performed a reanalysis of the vegetation data collected by Metzger (2002), and found significant variation in herbaceous plant cover across the rainfall gradient, from completely bare soil to densely formed grass mats. The general trend for herbaceous vegetation was that the mean % cover decreased with rainfall (% cover = $-0.88 \times \text{rainfall} - 26.3$; $F_{1,173} = 113.7$; $P < 0.001$; $r^2 = 0.40$). This was consistent with McNaughton (1985), who reported that grasslands transitioned from densely packed short-grasses

in the southern plains to sparser, larger-stature vegetation in the northern Serengeti. To investigate spatial variance in plant cover among different regions of Serengeti, we compared the average CV of herbaceous plant cover in the Serengeti plains, the western corridor, and the northern corridor (Gerreshiem regions 14, 9, and 7, respectively; fig. 5.2, panel B). Average CV was calculated from 20 randomly located plots that were approximately equidistant within each region. Plots were composed of nine subsamples in an evenly spaced 100 m² grid. The mean CV of herbaceous plant cover was over twice as high in Serengeti plains than in either the western corridor or the north (region 7 = 6.6; region 9 = 4.2; region 14 = 16.7; $F_{2,57} = 15.2$; $P < 0.001$; $r^2 = 0.34$). Moreover, when the CV of plant cover for each plot was regressed against mean annual rainfall, the relationship was linear and negative (CV plant cover = $-0.28 \times \text{rainfall} + 29.9$; $F_{1,58} = 21.1$; $P < 0.001$; $r^2 = 0.27$).

Unlike herbaceous vegetation, mean tree density increased linearly with rainfall (tree density = $0.009 \times \text{rainfall} - 0.39$; $F_{1,58} = 81.1$; $P < 0.001$; $r^2 = 0.31$). When the CV of tree density was compared among the Serengeti plains, western corridor, and the north, the Serengeti plains were almost an order of magnitude lower than the other regions (region 7 = 1.5; region 9 = 1.2; region 14 = 0.16; $F_{2,53} = 8.9$; $P < 0.001$; $r^2 = 0.25$). In contrast to understory herbaceous vegetation, when the CV of tree density for each plot was regressed against rainfall, the relationship was positively linear (CV tree density = $0.02 \times \text{rainfall} - 0.61$; $F_{1,54} = 7.0$; $P = 0.01$; $r^2 = 0.12$).

To estimate the spatial variance of soil and plant characteristics in Serengeti, we conducted a reanalysis of data collected by Anderson (2004) that included eight variables from 16 plots across the rainfall gradient. Plant variables were above- and belowground biomass, leaf and root nitrogen, and soil variables were inorganic nitrogen, % sand, pH, and % water. Plots were paired at eight sites, and sites were nested within four of the ten Gerreshiem regions. As a measure of variation at different spatial scales, the among-sample variance was calculated within plots ($n = 9$), sites ($n = 18$), regions ($n = 36$), and the entire data set ($n = 144$), after which the variance was averaged at each scale. To control for the effects of different sample sizes, sample variance at each spatial scale was estimated by resampling the data in 10⁴ plots using the freeware program PopTools (Hood 2004). Resampling is commonly used to reduce the bias created by different sample sizes and is a common procedure for hypothesis testing in ecology (Gotellie and Graves 1996).

Heterogeneity of soil and plant characteristics in Serengeti largely supports the ideas of fig. 5.1. The structure of variation across scales depends

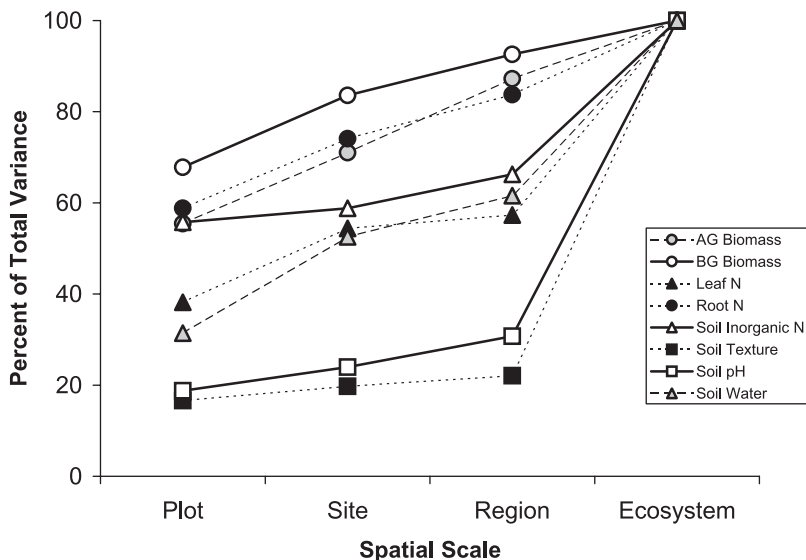


Fig. 5.4 Average variance of eight biotic and abiotic variables measured in 16 plots at eight sites across Serengeti (fig. 5.3). Variance was calculated within plots ($n = 9$), within sites ($n = 18$), within regions ($n = 36$), and among all plots ($n = 144$). To control for the different sample sizes among study scales, variance was calculated after the data were resampled 10^4 in PopTools (Hood 2004). Abbreviations in the legend are AG = aboveground, BG = belowground, N = nitrogen. Variables of the same symbol (circles, triangles, squares) have a similar pattern of variance across spatial scales. Only soil-inorganic N appears to not fall clearly into one of the groups.

on the variable considered, with the results generally conforming to three patterns (fig. 5.4). For the abiotic factors of soil texture and pH, most of the variation exists at the ecosystem level, with less of the total variation explained at the plot or regional scale. This is due to the geological origin of the parent material, as discussed later in the chapter. The remaining biotic factors vary over smaller spatial extents. For aboveground biomass, belowground biomass, and root%N, most of the total variation is explained at relatively small scales, with a small but consistent increase in the proportion of variance explained at larger scales (fig. 5.4). For leaf%N, soil inorganic N, and soil water, the situation is slightly more complex; these factors show some local and ecosystem variation, but little of the variance is explained by intervening scales. For these factors, there is a plateau in the proportion of variance explained between scales, such that increasing spatial scale has a small effect compared to the other scales; for soil inorganic N this occurs between plots and sites, for soil water and leaf N it occurs between sites and regions. Thus, organisms experience variation in leaf biomass and nutrients over smaller distances than factors such as pH or soil texture.

The variation at these sites demonstrates the difficulty of describing heterogeneity based on a single variable. For example, at TOG 2, variation in aboveground biomass was the lowest of any of the 16 plots studied (s^2 TOG 2 = 1,446; mean s^2 without TOG 2 = 17,176), but variance in leaf nitrogen was the largest of any site (s^2 TOG 2 = 0.28; mean s^2 without TOG 2 = 0.06). So an herbivore foraging within this site is met with two very different types of plant variation, namely, relative constancy in plant quantity but variation in plant quality. To help visualize the structure of variation across the ecosystem, the within-site variance of the eight variables, plus a measure of within-site topographic variance, were ordinated with nonmetric multidimensional scaling (Minchin 1987) in version 4.01 of PCORD (McCune and Medford 1999). Ordination is informative in this case because sites that occur near each other in multivariate space have similar patterns of variation for the nine variables. Variation in % sand, soil water, and aboveground biomass best separated the sites along the first ordination axis, while variation in aboveground biomass, topographic relief, and belowground biomass were most correlated with separation on the second axis. However, a plot of the first versus the second ordination axis demonstrated a lack of consistent within-site or within-region variation (fig. 5.5): adjacent plots tended not to group together and in no case were plots within the same site

NMDS Ordination Results: Variance of Nine Variables

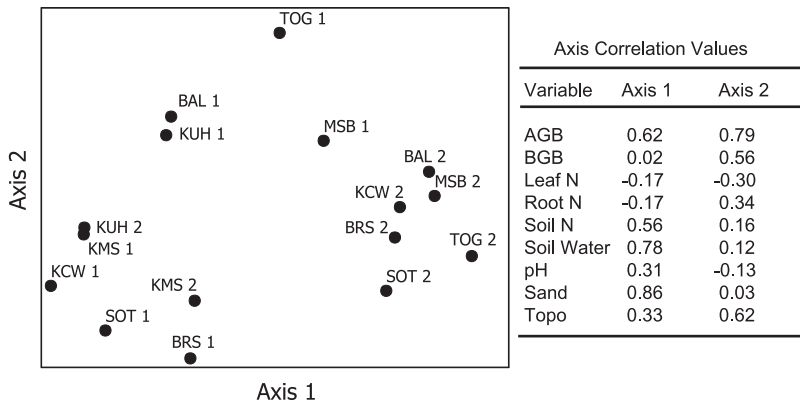


Fig. 5.5 Ordination results from nonmetric multidimensional scaling (NMDS) of variance measures within 16 plots at sites across Serengeti (see fig. 5.3). Variables used in the ordination are as in fig. 5.3, with the addition of topographic variation (Topo). Correlations between variables and axes one and two are shown to the right of the ordination plot. The results show a lack of within-site and within-region correspondence of heterogeneity; patterns of heterogeneity are often more similar between plots separated by hundreds of kilometers, compared to adjacent plots. AGB = aboveground biomass, BGB = belowground biomass, N = nitrogen.

nearest one another. Overall, patterns of variation between plots at distant sites were often more similar than plots separated by just a few kilometers.

Patterned Variance

Reporting a variance does not represent the spatial or temporal structure of heterogeneity experienced by organisms as they navigate through their environment (Weins 2000). An autocorrelation statistic, such as semivariance, is often used to represent variation in space or time because it incorporates spatial or temporal information into the calculation of variance (Anderson, McNaughton and Ritchie 2004). Neighboring points in space or time may be more similar than distant points, unless the spatial or temporal variation is random, in which case variation is constant as a function of distance or time. Data from Anderson, McNaughton and Ritchie (2004) allow a comparison between spatial and patterned variance of resin-extractable NO_3^- between paired plots at the eight study sites from fig. 5.5. From their data, it is clear that variance without a spatial reference may not adequately portray the data structure. For example, within-plot variation of resin-extractable NO_3^- in TOG 1 and TOG 2 were similar (s^2 TOG 1 = 226; s^2 TOG 2 = 187), yet the spatial structure differed significantly (fig. 5.6). The semivariogram for TOG 1 suggests a random NO_3^- distribution, while the semivariogram for TOG 2, shows a clear spatial pattern; resources show spatial autocorrelation between 0–18 m, with patches of an average size of ≈ 18 m arranged randomly on the landscape. Likewise, MSB1 and MSB2 had similar within-plot variance in resin-extractable NO_3^- (s^2 MSB 1 = 479; s^2 MSB 2 = 491), but again the spatial structure differed considerably (fig. 5.6). The semivariogram of MSB 1 suggests an average patch size of ≈ 14 m, with patches randomly arranged on the landscape. The semivariogram of MSB 2 suggests a constant increase in variation with distance, as would be observed in a unidirectional gradient of soil resources.

Some processes show spatial patterns that are self-similar across scales or scale invariant. This phenomenon is typical in natural landscapes, such as when the spatial distribution of vegetation cover or river networks is viewed at different scales (Milne 1992). Indeed, the pattern is evident for vegetation cover and river systems in satellite and aerial images taken of Serengeti at different spatial scales (fig. 5.7). When the distribution of a variable is self-similar across scales the variable is said to have a fractal or fractal-like distribution (Sugihara and May 1990). The fractal dimension (D) of a resource occurring in a two dimensional plane varies between 0 and 2; D = 0 is a single point, D ≈ 1 indicate highly clustered and self-similar

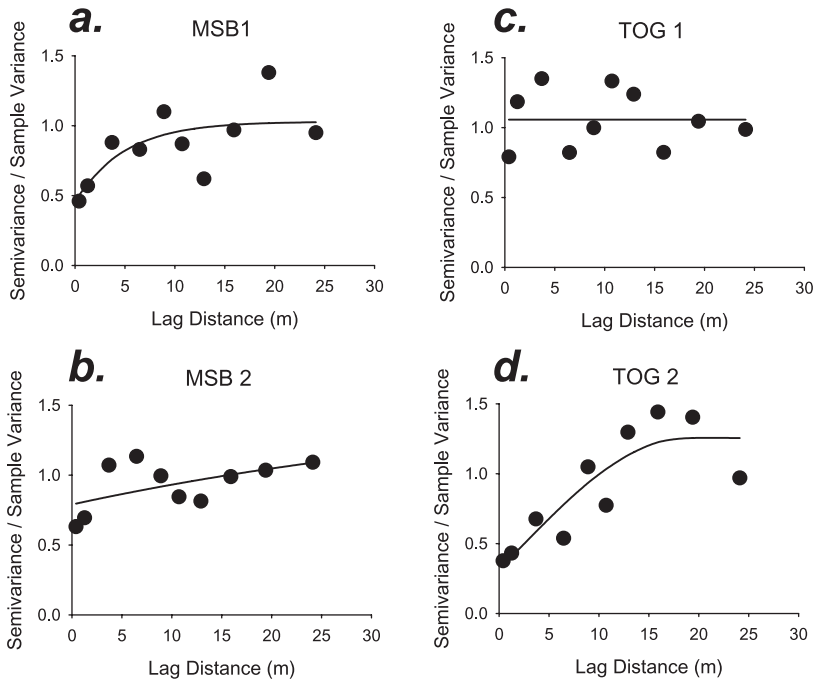


Fig. 5.6 Example semivariograms showing the average semivariance of soil NO₃⁻ availability as a function of separation distance. Soil NO₃⁻ availability was measured with 53 ion-exchange resin bags buried in each plot for one month after the beginning of the rainy season. Specific distance classes used to model semivariance are composed of multiple pairwise combinations of samples separated by a common distance; the number of sample pairs ranged between 30 at 0.4 m to 206 at 19.3 m. The examples shown compare adjacent plots at two sites, MSB and TOG (fig. 5.3). MSB 1 (A) shows spatial structure from 0–14 m, while MSB 2 (B) shows continuous increase in variance as the separation distance between points increases. At TOG 1 (C), the data showed no spatial structure, while at TOG 2 (D) there was spatial autocorrelation between 0–18 m. The distance at which the semivariance levels off, 14 m for MSB 1 and 18 m for TOG 2, is an estimate of the average NO₃⁻ patch size in the plot. TOG 1 shows no patch structure and MSB 2 suggests a continuous NO₃⁻ gradient. Data are from Anderson, McNaughton, and Ritchie 2004.

distributions, while $D \approx 2$ more completely fill the plane and are likely indistinguishable from a random distribution (Milne 1997). The analysis of semivariance and fractals are linked because D can be obtained from a log-log plot of the semivariance versus distance, where a positive slope (m) indicates a fractal dimension with $D = 2 - m/2$. The analysis of soil-NO₃⁻ spatial distributions between 0.4–26 m at multiple sites in Serengeti demonstrated that fractal and random distributions were equally common and often occurred in adjacent plots (Anderson, McNaughton and Ritchie 2004). Thus, resources occur in a complex mosaic of random and fractal distributions embedded within a landscape that has self-similar properties (vegetation cover, rivers, topography) across scales (fig. 5.7).

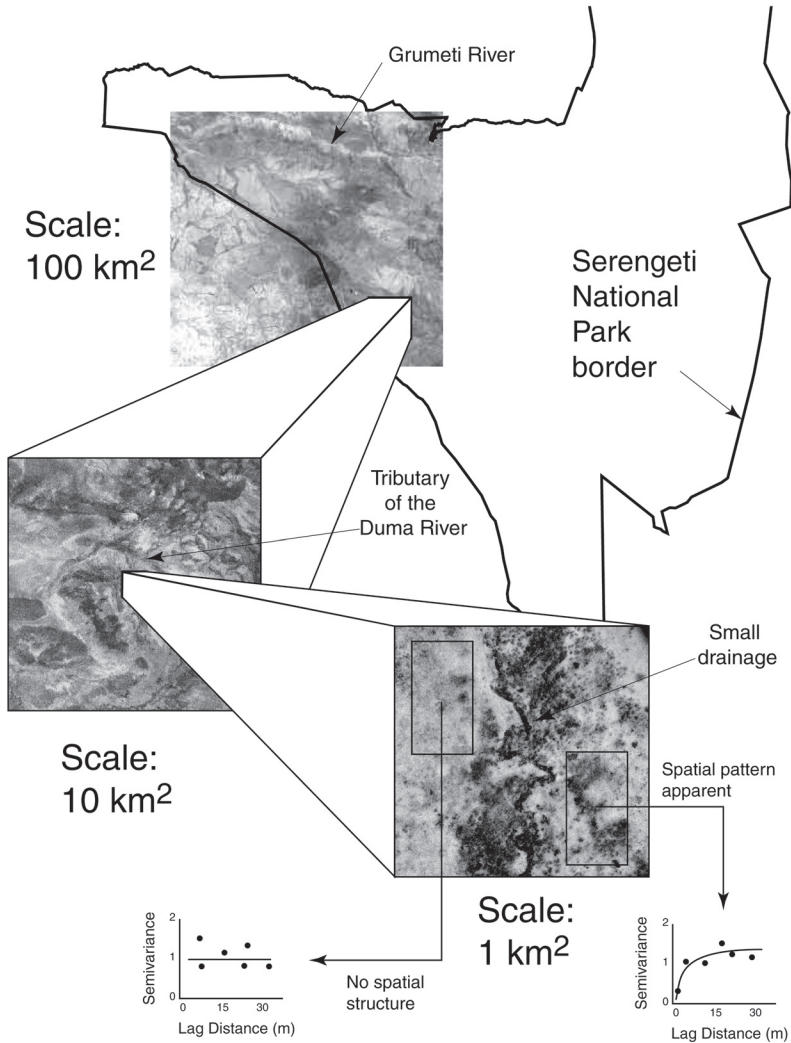


Fig. 5.7 Heterogeneity of vegetation cover and river systems across spatial scales. Three levels of spatial resolution are shown, 100, 10, and 1 km². 100 and 10 km² scales were extracted from Landsat 7 satellite images, 1 km² scale is from an aerial photograph. Although the images show disparate spatial scales, they share similarity in patterns of vegetation cover and river systems. The black rectangles embedded in the 1 km² image represent the different hypothetical patterns of heterogeneity, as were measured in adjacent plots in this study. The rectangle on the left lacks spatial heterogeneity, and therefore has a flat semivariogram. The rectangle on the right shows a self-similar pattern of heterogeneity across scales, and thus has a semivariogram that shows spatial structure. When taken together, one can see that heterogeneity exists in a complex continuum of random and structured features that exist on an equally complex template with self-similar characteristics across scales.

Summary of the Patterns

We now revisit the question put forth in the beginning of this section: what is the structure of heterogeneity across the Serengeti? In terms of compositional variation, heterogeneity in vegetation type (grasslands, woodlands, shrublands) increases with rainfall and topographic variation in the north and western corridor. Measured by plant β -diversity, the north, central hills, and western corridor are more heterogeneous than the regions dominated by plains to the south. Topography, geology, and grazing intensity also vary along the same gradient, and evidence from many sources suggests that compositional variation is linked to all these sources (see the following sections). In terms of spatial and patterned variance, the review emphasized grassland communities, so we limit our conclusions to those habitats. Our analysis revealed a common property of Serengeti grasslands: communities with substantial variation or complex spatial patterns were often adjacent to communities with modest variation and more-or-less random spatial patterns. Moreover, ordination results showed that sites on opposite ends of the ecosystem, separated by hundreds of kilometers, often displayed greater similarity in patterns of heterogeneity than sites within a few kilometers. Thus, heterogeneity is a universal property of the Serengeti, not restricted to regions that appear more complex because of differences in vegetation or topography.

AGENTS OF HETEROGENEITY IN SERENGETI

There are numerous processes that generate and maintain heterogeneity in African savanna ecosystems, but which are the most important in promoting the rich faunal and floral diversity observed in the Serengeti? In this section, we review the major agents of heterogeneity in Serengeti, focusing on those factors that have received the most attention and for which there are available data.

Abiotic Factors

Climate

At the largest scale in the Serengeti ecosystem, the influence of the inter-tropical convergence zone creates a bimodal pattern of rainfall: short rains, lasting from November to December, and long rains, lasting from March to May (chapter 2, this volume). However, other climate processes produce

rainfall patterns and variability in Serengeti, including continental heat lows, orographic rainfall, convergence rainfall, and local convection rainfall (Bell 1979; Prins and Loth 1988; Swift 1996). Lake Victoria, the massive water body to the west of Serengeti, creates a small convergence zone that produces dry-season rainfall in the zone surrounding its eastern shores (Sinclair 1979; Swift, Coughenour, and Atsedu 1996). Localized rainfall is higher in regions of significant elevation change, such as the hills in the north and western corridor (Wolanski and Gereta 2001). The Serengeti plains west of the crater highlands typically receive $< 500 \text{ mm yr}^{-1}$ rainfall because they sit in a rain shadow created by the Ngorongoro highlands. Convection events create local thunderstorms that can be intermittent and highly isolated. Because of Lake Victoria and orographic effects, dry-season rainfall variability is lowest in the north, intermediate in the western corridor, and highest in the Serengeti plains (Sinclair 1979).

To characterize climate variability in different regions of Serengeti, we analyzed 77 monthly rainfall measurements between the years 1985 and 1993 (chosen because they were relatively complete) for three rain gauge stations: Kogatende in the north, Ndabaka gate in the west, and the Serengeti plains in the south. We calculated the CV by months, seasons, and years to examine if a change in temporal scale of measurement influenced the results (fig. 5.8). Regardless of the temporal scale, rainfall CV was always lowest at Kogatende in the north. When analyzed by month, the data supported the findings of Norton-Griffiths, Helocker, and Pennycuick (1975), that low-rainfall areas have greater variability than high-rainfall areas; Naabi Hill in the Serengeti plains had the highest CV and the lowest monthly mean precipitation. However, dry-season CV over this time period was the greatest for Ndabaka in the western corridor, which also received the most rainfall. Annual rainfall CV was also greater at Ndabaka but only slightly greater than at Naabi Hill. Thus, the transitional habitat in the western corridor not only experiences abundant rainfall, but also significant variability at times likely to influence migration patterns of zebra and wildebeest.

While seasonal variability (dry/wet season) is largely predictable, the Serengeti experiences enormous variation in annual rainfall that is not correlated with the Southern Oscillation Index, as might be expected; only during an extreme El Nino event does the Serengeti receive predictably high annual rainfall (Wolanski and Gereta 2001). Support is provided by a recent hypothesis that suggests that climate patterns in East Africa can be explained largely by the Indian Ocean climate system (Webster et al. 1999). Climate variability has important effects on primary production across the whole ecosystem, but the effects of climate variability on primary production are probably stronger in low-rainfall areas (fig. 5.9; Oosterheld

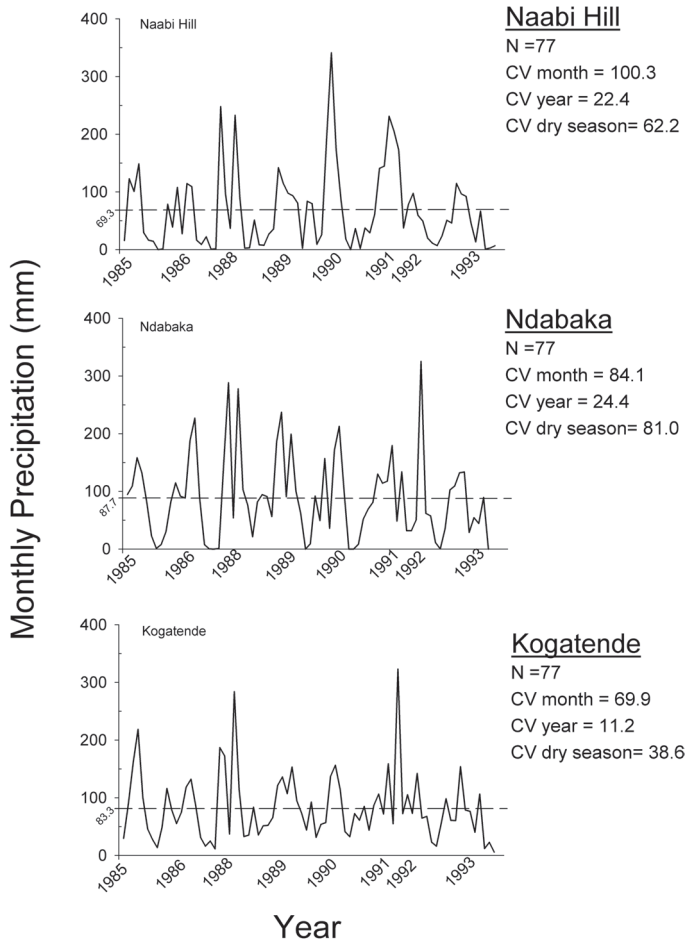


Fig. 5.8 Plots of monthly precipitation measures for three rain gauge locations in the south (Naabi Hill), the western corridor (Ndabaka), and the north (Kogatende) between 1985 and 1993 (see fig. 5.3 for rain gauge locations). Each plot has 77 months of data; when data were absent for one site, data were removed from all the sites for comparative purposes (note missing data between 1991 and 1992). Coefficients of variation (CV) were calculated by month, year, and dry season, and are listed for each site to the right of the plots. Mean monthly rainfalls are shown as dashed lines in each plot; the value is listed on the ordinate axis.

et al. 1999), such as the Serengeti plains. Behavioral models suggest that Serengeti grazers have adapted to stochastic temporal and spatial variation in rainfall and primary production by moving among grassland patches in ways that maximize their daily energy gains (Fryxell, Wilmhurst, and Sinclair 2004; Fryxell et al. 2005). Rainfall variability can affect plant species composition by influencing plant seedling emergence and recruitment (Veenendaal, Ernst, and Modise 1996a). Early rains can trigger multiple

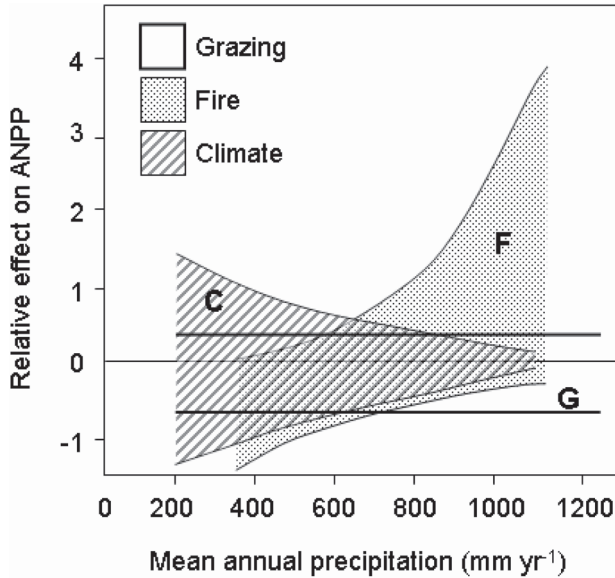


Fig. 5.9 The relative effects of fire (F), climate (C), and grazing (G) on annual net primary production (ANPP) across a range of mean annual precipitation in savanna-grassland ecosystems. Negative values represent a decrease in ANPP, while positive values represent stimulation of ANPP. Reprinted with permission from *Ecosystems of the World 16: Ecosystems of Disturbed Ground*, ed. M. Oosterheld, J. Loreti, M. Semmartin, and J. M. Paruelo. (1999). Grazing, fire, and climate effects on primary productivity of grasslands and savannas, pp. 287–306. The Netherlands: Elsevier.

emergence events, late rains can allow only a single emergence event, and early and late rains are associated with the emergence of different species (Veenendaal, Ernst, and Modise 1996b). Climate also has important effects on soil nutrient availability in Serengeti because the ability of soils to hold cations varies widely across the park. The soils of the western corridor and north are sandy, low in organic matter, and are easily leached of nutrients, while the soils of the Serengeti plains are silt-rich, have abundant organic matter, and are less easily leached (McNaughton, Ruess, and Seagle. 1988). Therefore, the rainfall patterns of Serengeti create a gradient of eutrophic to dystrophic soils typical of many African savanna systems (Huntley and Walker 1982).

Topography, Landscapes and Soil Composition

Soil heterogeneity in Serengeti is associated with parent material and landscape erosion processes. The broadest and most significant impact is historical and stems from Pleistocene and ongoing eruptions of natrocar-

bonatitic volcanoes in the Ngorongoro highlands (chapter 3, this volume, and Dawson 1964, Dawson et al. 1994; Hay 1976). During these eruptions, the same prevailing winds that structure the precipitation gradients carried ejecta west and north from their source, blanketing what are now the plains with sodium-rich ash. Finer ash particles were carried farther, creating a gradient in soil texture (de Wit 1978). On a more local level, soil texture varies across shallow topographic gradients. Hydrodynamic activity in conjunction with gravity creates local variability in soil characteristics along the repeated pattern of hills and valleys formed by drainage lines. This edaphic pattern, termed a *catena* (Milne 1935; Pratt and Gwynn 1977), influences the vegetation structure and species composition along its profile (Bell 1970; Herlocker 1976; Vesey-Fitzgerald 1973). Well-drained eluvial soils tend to dominate hilltops, giving way to finer textured soils on lower slopes and valley bottoms (de Wit 1978; Jager 1982; Yair 1990; Gerrard 1990).

Landscape variation is associated with variability in soil fertility (Scholes 1990; Venter, Scholes, and Eckhardt. 2003) and soil alkalinity (Belsky 1988, 1992; Coughenour and Ellis 1993) which in turn influence plant water-use efficiency, morphology, chemistry, and rates of plant herbivory and growth (Scholes 1990). For example, in nearby Lake Manyara National Park, shrubs growing on volcanic soils had significantly higher diameter growth rates and height increases, 2.65 % and 18.9 %, respectively, compared to diameter increase of 1.78 % and height increases of 12.1 % for shrubs growing on nutrient-poor soils derived from basement complex (Prins and Van der Jeugd 1992). Thus, the results of landscape and soil complexity across Serengeti contribute to vegetation heterogeneity among vegetation types (Anderson and Talbot 1965; Belsky 1988).

Landscape and soil heterogeneity may also contribute to species coexistence within vegetation types. Across the 1,000 m² plots studied by Anderson, McNaughton, and Ritchie (2004), greater topographic variation was associated with greater among-sample variance in soil texture. In turn, the number of plant species in plots increased with variation in soil texture (fig. 5.10), explaining a relatively large proportion of the sample variance. Thus, if plant species are adapted to different soil types, topographic variation can influence plant species richness by promoting opportunities for coexistence through greater habitat heterogeneity (Shmida and Wilson 1985; Anderson, Metzger and McNaughton 2007). In another example, landscape heterogeneity contributes to coexistence between the Serengeti's two dominant grasses, *T. triandra* and *Digitaria macroblephara*, by influencing soil texture. When exposed to simulated grazing, soil texture has opposite effects on the two species; *T. triandra* acquires more N in low-sand soils

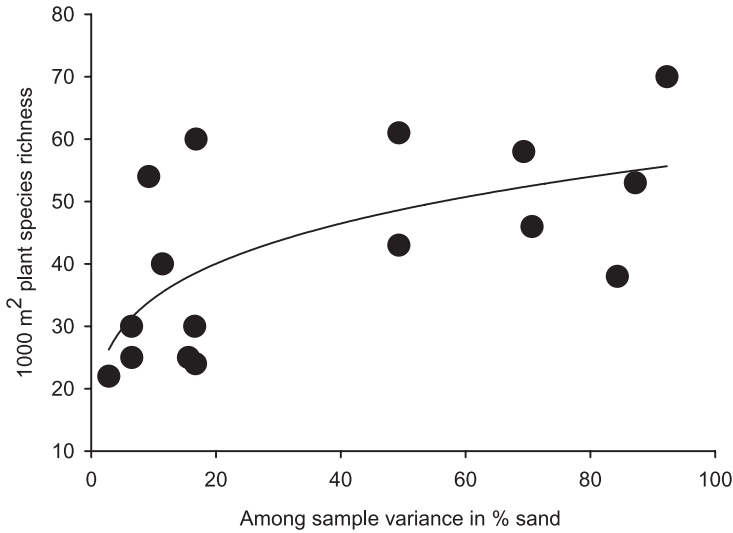


Fig. 5.10 Relationship of among-sample variance in % sand (from $n = 9$ subsamples from each plot) and corresponding plant species richness from 16 paired plots at 8 sites that span the Serengeti rainfall gradient (fig. 5.3). Samples were collected in 1000 m² plots at each site.

while *D. macroblephara* acquired more N in sandy soils (Anderson, Dong, and McNaughton 2006).

Across the Serengeti, variation among geographic land regions explained differences in soil microbial processes and nutrient cycling (Ruess and Seagle 1994). Soils with greater clay content were associated with greater electrical conductivity, pH, and water-holding capacity. As a result, soils with greater water-holding capacity and total carbon supported larger microbial populations with greater rates of respiration, N-mineralization, and carbon and N-turnover rates. As a consequence of regional landscape variation, soils in the Serengeti plains and western corridor had greater rates of biological activity and greater standing pools and nutrient fluxes than soils in the central hills and northern extension. Moreover, Ruess and Seagle (1994) linked the soil processes to higher trophic levels by demonstrating significant correlations between herbivore consumption and both soil microbial biomass and soil respiration rates, and between grazing intensity and rates of soil nitrogen mineralization.

Finally, granitic outcrops, such as kopjes, torrs, and inselbergs, provide unique habitat for organisms that cannot exist elsewhere, such as desiccation-tolerant vascular plants (Porembski and Barthlott 2000) and small-bodied ungulates, such as klipspringers. Moreover, kopjes provide protected foraging sites for elephants and other mammals (A. R. E. Sinclair,

pers. comm.). Bird diversity was significantly greater on kopjes than surrounding habitats and was composed of a unique community type that included species that were rare elsewhere in Serengeti (Trager and Mistry 2003). For hyraxes, dispersal among the rock “islands” by members of small populations decreases the colonies probability of local extinction (Gerlach and Hoeck 2001).

Fire

Fire acts as an important disturbance regime and is major factor determining savanna structure. It directly affects vegetation and ecosystem processes by creating a pattern of grass and woody biomass removal, destruction of aerial portions or killing of woody plants, nutrient volatilization, and enhancement of above-ground net primary productivity. A classic theory suggests that the coexistence of woody plants and grasses is controlled by the access of trees to moisture in deep-soil horizons and grasses to upper-soil horizons (Walter 1971). While not mutually exclusive of this theory, Higgins, Bond, and Trollope (2000) suggested that trees/grass coexistence in savannas is maintained instead because woody vegetation is more susceptible to high-intensity fires compared to quickly recovering herbaceous vegetation.

Fire generates heterogeneity because it does not occur everywhere, and where it does occur it does not burn uniformly. Heterogeneity that results from fire is the result of fire type, frequency, and intensity. Savanna fires are typically surface fires and either head fires spreading with the wind, or back fires spreading against the wind. Under otherwise similar conditions, head fires, which burn at high intensity and kill aerial portions of trees, can have very different effects compared to back fires, which burn at lower intensity but spread at a lower rate. Back fires threaten the grass sward more than head fires because high temperatures close to the ground are maintained for prolonged periods of time, resulting in damage to grass apical meristems (Trollope 1982).

Fire frequency depends on the availability of fuel, which increases monotonically with rainfall (Oesterheld et al. 1999). Fires rarely occur below 450 mm precipitation (Trollope 1974; Oesterheld et al. 1999); much of the Serengeti plains (regions receiving < 500 mm rainfall) burn infrequently. The relationship between rainfall and fire frequency is particularly strong in Serengeti ($r = 0.73$, $n = 150$; Norton-Griffiths 1979); moreover, within-year fire frequency is highly correlated with wet-season rainfall (fig. 13.8 in Norton-Griffiths 1979). Fuel availability is also controlled by the consumption of productivity by grazers; severe defoliation can reduce fuel

loads and lower fire frequency (Roques, O'Conner, and Watkinson 2001), an effect that is enhanced by high herbivore density (van Wilgen et al. 2003). Grazing increases with ANPP, but less so than biomass production, resulting in a positive correlation between unconsumed productivity or available fuel load and ANPP (Oesterheld et al. 1999).

Finally, intensity strongly influences the ecological impacts of fire (van Wilgen et al. 2003). Although fire intensity increases in plots with greater grass cover (Salvatori et al. 2001), it does not significantly influence the recovery of the grass sward (Trollope, Trollope, and Hartnett 2002). In contrast, fire intensity does have significant effects on woody vegetation and tree recruitment. Moreover, variance in fire intensity, created by variation in grass biomass, grazing, tree neighborhoods, and ambient conditions such as wind speed (Higgins, Bond, and Trollope 2000) produces variance in woody plant recruitment rates, which regulates tree/grass coexistence. Depending on intensity, fires can prevent tree recruitment by killing tree seedlings or seriously damaging the aboveground parts of shrubs and trees. Small trees can revert to a multistemmed, shrubby form that can be shaded by grasses and vulnerable to the next fire (Bond 1997). In Serengeti fires, Herlocker (*sensu* Norton-Griffiths 1979) reported that 92% of *Acacia* trees < 1 m were burned back to ground level, 68% of trees between 1–2 m, 28% of trees between 2–3 m, and 1% for trees > 3 m. Likewise, Norton-Griffiths (1979) found that in a *Combretum-Terminalia* woodland, fire burned back 94% trees < 1 m, 68% for trees between 1–2 m, and 45% for trees between 2–3 m. Even if young trees are not killed, they are unable to replace those lost to other factors, such as elephants, resulting in a woodland mosaic with patches of even-aged trees (Norton-Griffiths 1979).

For several months after the occurrence of fire, leaf nutrient concentrations are elevated in postfire vegetation. The increase results because of a greater ratio of leaf to stem, rejuvenation of plant material, and the distribution of similar nutrients in less aboveground biomass (van de Vijver, Poot, and Prins 1999). However, the effect of fire on nutrient heterogeneity has a complex interaction with other factors (van de Vijver 1999; Anderson et al., forthcoming); nitrogen and phosphorus concentrations in postfire vegetation depended on rainfall (wet vs. dry year), soil type (black cotton vs. lacustrine), and landscape position (ridge top vs. ridge slope). As a result of the increased live:dead ratio of leaves and increased plant nutrient concentrations, ungulates preferably forage in recently burned areas. But green flushes are not used equally by different species; there is a negative relationship between burn use and body size among ungulates (Wilsey 1996). This is because larger ungulates require large quantities of vegetation but can tolerate relatively poor-quality forage, such as occurs in unburnt

vegetation. Smaller ungulates, on the other hand, need less food volume but require relatively high quality forage (Illius and Gordon 1987), which is available in burnt grassland patches.

Biotic Factors

Grazing

Grazer effects on heterogeneity depend on the spatial pattern of grazing and the spatial pattern of the underlying vegetation (Adler, Raff, and Lauenroth 2001). On a regional scale, the dense wildebeest herds that graze intensively during the wet season in the Serengeti plains have created grazing lawns, a characteristic that results from both the reduction of the grass sward through defoliation and natural selection for prostrate, grazing-tolerant genotypes (McNaughton 1984). In contrast, less intensive and patchy grazing occurs in the mid- and tall grasslands that are utilized primarily during migration or localized rainfall (McNaughton and Sabuni 1988). On local scales, resident herbivores can maintain grazing lawns in heavy utilized areas called *hot spots* (see below) or around physical structures such as kopjes, trees, and termite mounds. Grazers can create spatial heterogeneity in grass sward height by selectively grazing patches of herbivore-tolerant species, such as *Cynodon dactylon*, and avoiding patches of unpalatable species, such as *Eleusine jaegeri*, as occurred in Arusha National Park (Vesey-Fitzgerald 1974).

In addition to effects on sward structure, Serengeti grazers can increase plant species richness (McNaughton 1983; Anderson, Ritchie, and McNaughton 2007), the mineralization rates of growth-limiting nutrients (McNaughton, Banyikwa, and McNaughton 1997), and primary production (McNaughton 1979, 1985). However, the generation of heterogeneity is increased because the modification of plant and soil characteristics by grazers often interacts with other factors that vary across the ecosystem. For example, overcompensation by plants in response to grazing that can lead to a stimulation of primary production requires a sufficient interval between defoliation events for regrowth to occur (Oosterheld and McNaughton 1991) and a threshold level of inorganic nitrogen (Hamilton et al. 1998). Evidence from other systems suggests that grazing alters plant demography in ways that apply to Serengeti, including effects on seed production (Anderson and Frank 2003), plant size (Butler and Briske 1988), age (Pfeiffer and Hartnett 1995), and density (O'Connor 1994). Herbivore density and body size appear to have important implications for the effects of grazers on heterogeneity in savanna ecosystems (Olf and Ritchie 1998;

Adler, Raff, and Lauenroth 2001; Bakker et al. 2004). Moreover, the interaction between plant tolerance and grazer forage selectivity can modify the influence of grazing on ecosystem processes and heterogeneity (Augustine and McNaughton 1998).

Various ungulate herbivores differentially promote heterogeneity. Hippos impact geomorphology by creating paths, aversions, levees, and swamps (McCarthy, Ellery, and Bloem 1998). In Serengeti, topi increase their efficiency and offtake of green leafy biomass by grazing selectively in grassland swards in which reproductive stems have developed, whereas wildebeest graze to a lower height, thus increasing their efficiency and offtake in short vegetative grassland swards (Murray and Illius 2000). This effect can vary with season, phenology, and plant quality; selection of grass swards by Roan antelope in South Africa shifted between high-quality forage in the late dry season and early wet season to high quantity in the late wet and early dry season (Heitkonig and Owen-Smith 1998).

Browsing

Landscapes represent a continuum of spatially heterogeneous resources across a hierarchy of scales for all organisms. For browsing ungulates, the hierarchy, from small to large, might be leaves, twigs, branches, trees, and woodland patches (Skarpe et al. 2000). The attributes of each level in the hierarchy can influence browsing selectivity, such as chemical defense of leaves, spines that occur on twigs, and species abundance in a woodland patch, attributes that influenced browsing selectivity in woodlands in Botswana (Skarpe et al. 2000). Small browsers, such as impala, Grant's gazelle, Thompson's gazelle, and dik-dik were implicated in a study of the effects of browsers on woodland regeneration in Serengeti (Belsky 1984). In the study, browsing significantly reduced tree heights at a mid-grass site and tall-grass site near Lobo and kept regenerating trees in the smallest size class for the entire three-year study.

Even though tree density varied widely in Serengeti woodland and riverine habitats, browsing and damage by elephant and giraffe was not related to the density of trees in a stand (Ruess and Halter 1990). Moreover, for the majority of tree species sampled, browsing damage occurred in direct proportion to their occurrence, suggesting that most species were selected more or less at random. However, *A. senegal* was significantly preferred in one stand, *Commiphora trothae* and *A. clavigera* (now *A. robusta*) were significantly avoided in several stands, while *Acacia tortilis*, *A. xanthophloea*, and *Albizia harveyi* were always damaged in proportion to their occurrence. As with the stimulation of herbaceous biomass by grazers, the removal of

shoots by simulated giraffe browsing stimulated shoot production in *Acacia tortilis*, *A. xanthophloea*, and *A. hockii* (Pellew 1983). The impact of browsing on vegetation varies seasonally, with the most significant impact happening during the green flush that occurs approximately 1 month prior to the onset of the November rains (Pellew 1983).

Elephant have the greatest influence of any browsing mammal in Serengeti, and their behaviors have been at the heart of a controversy surrounding woodland decline for decades (Lamprey et al. 1967; Norton-Griffiths 1979). Their main direct effect on vegetation is to increase mortality by uprooting mature trees and stripping bark and to reduce recruitment of seedlings by consuming them. In the Maasai-Mara Reserve, elephants increase woodland fragmentation by removing branches and creating paths in woody thickets (Dublin 1995). However, their role in woodland degradation may be overstated; elephants largely consume grass (Croze 1974a, 1974b) and most moderately damaged trees survive (Sinclair 1995). Moreover, a study from a Kenyan savanna ecosystem demonstrated that *Acacia drepanolobium* seedling survival was lower in the absence of large mammalian herbivores (Goheen et al. 2004). Apparently, elephants and other large herbivores suppressed herbivory by small mammals and insects that decreased seedling mortality. In the same savanna, results of an enclosure study suggested that small browsers, such as dik-diks, had a major influence on suppressing shrub recruitment through selective browsing (Augustine and McNaughton 2004).

Termites

Unfortunately, termites themselves have gone largely unstudied in the Serengeti, perhaps because of the significant research emphasis on ungulates and carnivores. However, studies of vegetation (Glover, Trump, and Wateridge 1964; Belsky 1983) and soils (de Wit 1978) in the Serengeti region identified termites, termitaria, and abandoned mounds as significant determinants of vegetation pattern, species composition, and functional type (e.g., perennial, annual, short-grass, tall-grass). Total consumption of plant biomass by termites increases with rainfall, a pattern that has been observed among (Deshmukh 1989) and within (Buxton 1981) African savanna ecosystems. However, the proportion of total primary production that is consumed by termites is believed to decrease with increasing rainfall (Deshmukh 1989). Despite the presence of a strong rainfall gradient and abundant termite populations, whether these ecologically important relationships hold for Serengeti is not known.

The results of research from elsewhere in Africa have provided consid-

erable insight into termite impacts in savanna ecosystems and have highlighted their role as ecosystem engineers. For example, in central Tanzania, the density and type of termites was one of the strongest indicators of soil depth, texture, clay mineralogy, drainage, and parent material at the regional level (Jones 1989). Different termite species have different life-history strategies, such as energetics, spatial distribution, nest-building, and habitat, which can have different effects on the surrounding environment (Eggleton and Tayasu 2001). Termite diets consist of dead plant material, leaf litter, woody debris, and dung (Dangerfield and Schuurman 2000) but can vary depending on species. The mounds of similar species, such as harvester ants (*Messor capensis*) in South Africa, can act as centers of plant germination and diversity and can improve seed production and growth rates of plants growing on compared to off mounds (Dean and Yeaton 1993). Moreover, harvester ant mounds disturbed by aardvarks contained a greater number of viable seeds for germination than soil between mounds, and seed germination on mounds varied significantly in time in a way that depended on rainfall (Dean and Yeaton 1992).

One conspicuous influence of termites is their effect on soil chemical and physical properties. First, termites mix soil layers within their nests by translocating small soil particles to the surface (Holt and Lepage 2000). Second, termites act literally as agents of weathering by increasing the expandable clay minerals in the soil used to build chamber walls in a more-or-less irreversible way (Jouquet et al. 2002). In terms of their effects on soil chemical properties, the presence of termite mounds results in the accumulation of bases in the surrounded soils (Malaisse 1978). In South Africa, soils of eroded termite mounds were more acidic and enriched in Mg, Ca, N, P, and total exchangeable cations compared to soil in between mounds. Moreover, the differences in soil nutrients translated into greater primary production and leaf % nitrogen in *T. triandra* that was grown on soils from eroded termite mounds compared to control soil (Smith and Yeaton 1998).

Individual Trees

Individual trees occurring in savannas change the light, nutrient, and water conditions in their immediate vicinity, as well as offer physical refuge for a wide variety of organisms such as ungulates, carnivores, birds, reptiles, amphibians, and insects. The influence of savanna trees on understory vegetation in Kenya was positive via effects of shading reducing water stress and increasing nutrient availability (Weltzin and Coughenour 1990). Belsky et al. (1993) demonstrated that tree canopies decreased ambient light levels, soil temperatures, and soil C:N ratios, but increased organic matter

and soil nutrient availability (total N, P, K, and Ca). Moreover, grassland production was higher under tree canopies at xeric sites compared to mesic sites, an effect believed to result from the higher benefit that reduced shade confers to grasses in xeric conditions compared to mesic sites. Belsky (1994) showed that herbaceous production in open grassland was nutrient limited compared to underneath trees, and that higher productivity resulted from increased nutrient inputs from trees. Furthermore, she suggested that water competition was reduced at arid sites because tree roots exploited soils farther from the tree and thus did not compete with grasses near the tree base, but competition for water limited herbaceous production at mesic sites. Amundson, Ali, and Belsky (1995) found that shade benefited crown species such as *Cynodon nleemfuensis* and *Panicum maximum* because they could close their stomata in response to shade and thus conserve water. On the other hand, grassland-zone species such as *D. macroblephara* and *Eustachys paspaloides* were unable to alter stomatal conductance in response to reduced light.

In Tarangire, trees effectively shifted nutrient limitation from N-limited in open grassland to P-limited under tree canopies (Ludwig et al. 2001, Ludwig, Dawson et al. 2004). Moreover, N:P ratios of grasses under small trees were intermediate to N:P ratios of grasses in open grassland and under large trees, suggesting that the shift from N- to P-limitation happens gradually (Ludwig, Dawson et al. 2004). In the mid-wet season nutrient concentrations of grasses were higher under tree canopies, suggesting that grass production was limited by light, when water and nutrients were abundant. However, canopy shade had positive effects on grass productivity in the dry season when water was scarce (Ludwig et al. 2001). For biomass and diversity were highest under tree canopies because of their tolerance for shade. Herbaceous vegetation was greatest under dead trees and was on average 60% more than under live trees, providing further evidence that trees and herbaceous vegetation compete for water. Finally, in support of Belsky's (1994) findings, Ludwig, de Kroon et al. (2004) showed that, even though hydraulic lift occurs under *Acacia tortilis* (Ludwig et al. 2003), competition between grass and trees overwhelms the positive effects of lift in African savannas.

Herbaceous Vegetation

While soils exert obvious effects on vegetation, plants also exert reciprocal effects on soil. Plants alter nutrient cycling (Wedin and Tilman 1990) soil microbial processes (Groffman et al. 1996; Hamilton and Frank 2001), and soil fertility (Ludwig et al. 2001). Small-scale variation in NO_3^- was corre-

lated with local species diversity across grassland sites, suggesting that plant species directly influence nutrient concentrations in the small soil volumes surrounding plants roots (Anderson, McNaughton, and Ritchie 2004). Grasses in Serengeti are associated differentially with vesicular-arbuscular mycorrhizae fungi, which are more abundant at nutrient poor-sites and which may buffer plant nutrient quality against poor-quality soil (McNaughton and Oesterheld 1990). Plants with different life history strategies and growth forms (i.e., annuals, perennials, grasses, forbs, and shrubs) differ with respect to root and leaf tissue chemistry and elemental stoichiometry in ways that influence decomposition, soil mineralization, and microbial dynamics, all of which create plant-derived heterogeneity (Hobbie 1992). Belsky (1986) attributed small-scale vegetation patchiness in the Serengeti plains to the vegetative growth habits of dominant grasses, which form stable patches for long periods of time.

Recent studies reveal the profound impacts that temporal and spatial variation in primary production has on the movements and population dynamics of large-bodied Serengeti mammals. For example, the local movements of Thompson's gazelles among patches of herbaceous vegetation suggest they adaptively locate patches that maximize their energy intake (Fryxell, Wilmhurst, and Sinclair 2004; Fryxell et al. 2005). The population dynamics of Serengeti lions depend on variation in primary production because tall vegetation provides cover for hunting lions, thereby increasing the accessibility of prey (Hopcraft, Packer, and Sinclair 2005). Moreover, extreme climate events that cause substantial or sustained changes in herbaceous vegetation can trigger salutatory changes in the size of the lion population that remain stable on decadal time scales (Packer et al. 2005).

Human Impacts

People induce heterogeneity in vegetation and landscape patterns in Serengeti at different spatial and temporal scales and through a variety of processes. Fire is used to alter grassland/woodland mosaics or as a management tool. Grazing by domestic stock influences heterogeneity. At a more local scale, individual settlements, roads and paths, and cultivated land fragment the landscape. Written accounts from early explorers and settlers, and later on maps and aerial photographs allow for a reconstruction of the Serengeti landscape over the past 100 years. At the turn of the century, explorers, traders, and hunters described the Serengeti as open grassland with lightly wooded patches. The rinderpest pandemic of the 1890s devastated both domestic and wild ruminants and vegetation composition and landscape patterns changed drastically in the years that followed. By the time

the colonial administrators arrived in the 1930s and early 1940s, the area had become densely wooded and infested with tsetse flies and trypanosomiasis (Lamprey and Waller 1990; Dublin 1995). From the 1950s onward, a combination of increased wildebeest numbers and high fire frequency (both natural and induced by the Maasai) led to the rapid disappearance of the woodlands, to make place for grazing lawns once more. Lamprey (1984) analyzed changes in woodland cover in three areas of the Mara from 1950 to 1983 and found that in all sites, woody cover had declined from 20–35% in 1950 to less than 10% by 1974. By the 1980s, woodland cover recovered at one of the sites, while it further declined at the second site and trees completely disappeared from the third site.

People also have a profound impact on the land through the development of permanent settlements and agriculture. Serneels, Said, and Lambin (2001) studied natural and anthropogenic changes in vegetation cover in and around the Serengeti between 1975 and 1995 using satellite imagery (fig. 5.11). The analysis demonstrated that the most important single type of land cover change was due to conversion to agriculture, ranging from small patches of subsistence cultivation (e.g., in NCA highlands) to large areas under mechanized farming (e.g., Loita plains; see Homewood et al. 2001). Although small, isolated patches of agriculture will at first increase the structural heterogeneity of the landscape, beta-diversity decreases when natural vegetation is replaced by one crop. As agriculture spreads, the structural heterogeneity is lost, too. This has implications for wildlife, as grazing/browsing resources are no longer available, and migration routes can become blocked. Mechanized farming in the Loita plains in Kenya spread from 4,875 ha in 1975 to 50,000 ha in 1995, resulting in the destruction of calving habitat for resident wildebeest population and a subsequent 70% population decline since the late 1970s (Ottichilo, de Leeuw, and Prins 2001; Serneels and Lambin 2001; Serneels, Said, and Lambin 2001). In recent years, the fields in the dryer parts have been abandoned, due to a combination of unfavorable weather conditions and land privatization. Activities are being shifted to irrigated agriculture on the banks of the Mara River. Since 2003, several new enterprises are drawing water from the Mara River, which may have consequences for wildlife in drought years (Gereta et al. 2002).

Other land changes in the northern Serengeti include the expansion of settlements of smallholders, mostly around the gates of the Maasai-Mara at Talek, Sekanani, and Aitong, including an increase in the number of Maasai settlements (Lamprey and Reid 2004) and their associated decrease in vegetation cover, and small-scale maize farming. The Maasai and similar nomadic peoples protect livestock in high animal density enclosures called

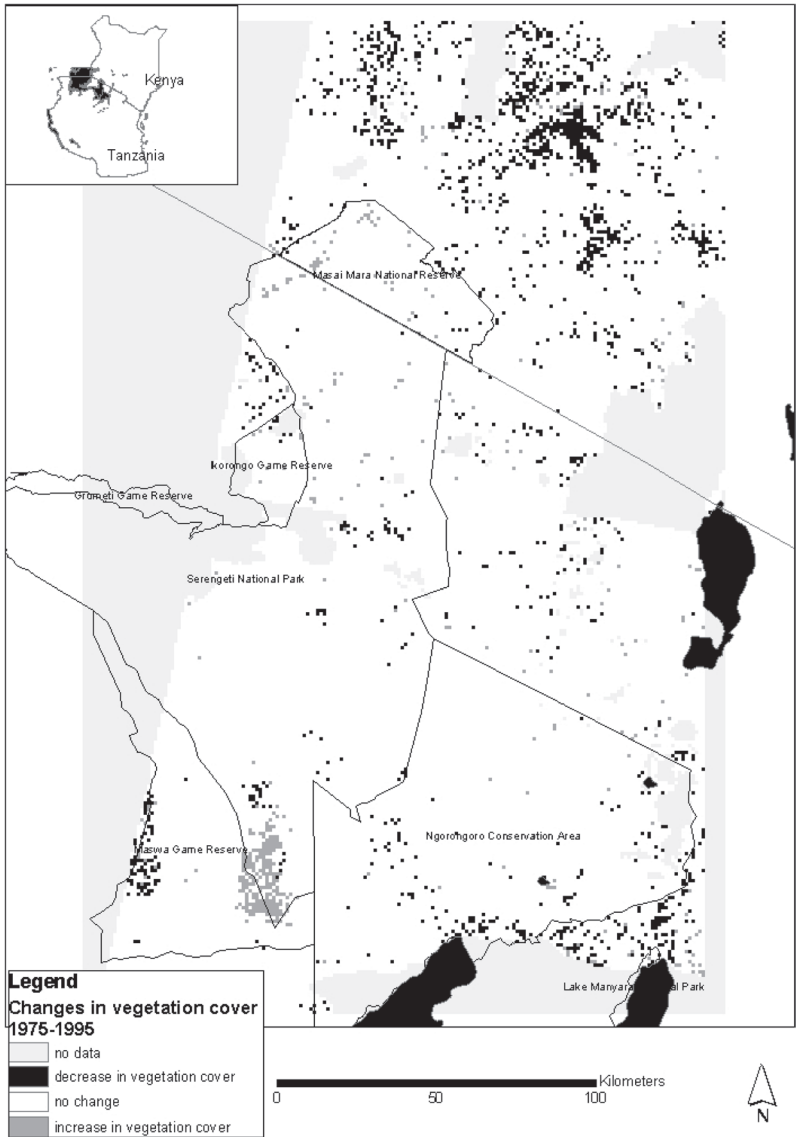


Fig. 5.11 Changes in vegetation cover in the Serengeti ecosystem as detected from a time series of Landsat images from 1975–1995. Pixel colors indicate land cover change: light grey = no available data; dark grey = increase in vegetation cover; black = decrease in vegetation cover.

bomas. While they are only temporary, significant dung and urine is deposited during occupation. People preferably settle in areas that present a number of advantages to them, such as proximity to permanent water (Reid et al. 2003), or with potential revenues from or employment in the tourism sector (Thompson 2002). These hot spots are also of key importance to wildlife, and a source of wildlife-people conflicts and habitat destruction. Several studies (Walpole 2002; Boydston et al. 2003) have shown changes in animal behavior in the Maasai-Mara, due to settlement expansion around the park boundaries. In 1970, the rangelands north of the Maasai-Mara were converted to group ranches under communal Maasai ownership and management. In 1999, Lemek Group Ranch was subdivided into private parcels, and currently the same process is ongoing in Koyaki Group Ranch, bordering the Maasai-Mara. An early manifestation of subdivision was the fragmentation of the traditional boma into one- or two-family units, and the proliferation of these new homesteads within their localities (Lamprey and Reid 2004). This increasing number of bomas effectively fragments the landscape, as wildlife behavior is altered by their presence.

CASE STUDIES: MULTIFACTOR INTERACTIONS AND HETEROGENEITY IN TIME AND SPACE

Elephants, Fire, Grazing, Humans, and Woodlands Dynamics

Over the past one hundred years, the Serengeti-Mara ecosystem has experienced major changes in woodland vegetation; grasslands transitioned into woodlands from 1890s to 1940s and back from woodlands to grasslands in the 1960s to 1980s, a trend that continued in the Maasai Mara but reversed in the northern Serengeti during the 1990s (Dublin 1995, and see chapter 2, this volume). The major factors attributed to woodland change have been fire, elephants, and grazing. However, assigning causation to any one factor has been problematic, because factors interact and are difficult to measure because of their dynamical nature. Between 1963 and 1972 the Serengeti lost 13% of its woody cover; the largest part of this occurred in northern Serengeti and Maasai-Mara (26%), compared to lower degradation in the central woodlands (7%). Moreover, the reduction was not uniform: woody vegetation cover showed a blanket decrease in the north, changes in woody cover showed a heterogeneous mosaic of increase and decrease in the central woodlands (Norton-Griffiths 1979).

Analysis suggested that fire was most strongly associated with reduction in woody cover in the north, while the dry-season elephant population size was most strongly associated with woody vegetation reduction in the cen-

tral woodlands. Dublin, Sinclair, and McGlade (1990) showed by using a simple model derived from data on wildebeest, fire, elephants, and browsing antelopes, that the combined effect of elephants and fire had the greatest impact on Serengeti-Mara woodlands. They convincingly argued that high fire frequency was responsible for woodland decline during the 1960s, while high elephant densities maintained the grassland state throughout the 1980s. Apparently, human-induced fires were common during this period, and fires intensified because of the large fuel loads that followed the ungulate population declines during the rinderpest outbreak (Dublin 1995). However, after the eradication of rinderpest, the wildebeest population underwent a sixfold increase in just over 10 years (Sinclair 1995), resulting in the elimination of much of the fuel for fires, thus reducing the intensity and frequency of fires. By reducing fire damage to seedlings grazing may actually increase the potential for woodland regeneration.

Yet even after the drastic reduction in fire frequency, grassland states were maintained and existing woodlands continued to decline throughout the 1980s. Dublin, Sinclair, and McGlade (1990) showed that the best explanation lay in the burgeoning elephant population, especially in the northern Serengeti and Maasai-Mara. It was suggested that elephants act synergistically with fire, by opening up woodland thickets and canopies so that herbaceous fuel loads increase and fire damage is worsened, a scenario that was observed in Croton thickets in the Maasai-Mara reserve (Dublin 1995). Recently, trends in woodland cover in the Serengeti central hills region have reversed, while woodlands have continued to decline in the Maasai-Mara. Apparently, antipoaching efforts and high visitation rates have allowed high elephant densities in the Maasai-Mara, while the threat of poaching in the central hills keeps elephant densities relatively low.

Hot Spots: Formation and Maintenance

Resident herbivores in Serengeti are not distributed evenly across the ecosystem. Instead, they often occur in “hot spots,” areas of high-density mixed herds, found in regions receiving greater than 700 mm yr^{-1} rainfall (McNaughton 1988). Hot spots are spatially and temporally stable for over 20 years, but they are heterogeneously distributed in the Serengeti ecosystem. Forage nutrient concentrations in hot spots are greater than in adjacent grasslands with low ungulate densities; magnesium, sodium, and phosphorus, important for ungulates during late pregnancy and lactation, occur in concentrations that meet dietary requirements in hot spots

but not in adjacent unused grasslands (McNaughton 1988). Moreover, experiments showed that soil mineralization rates of sodium and nitrogen were higher in ungulate high-use areas, and that ungulate grazing actually promoted increased sodium mineralization rates by as much as an order of magnitude (McNaughton, Banyikwa, and McNaughton 1997). Therefore, grazing ungulates choose hot spots of greater leaf tissue nutrients and forage quality that occur heterogeneously across the landscape, and grazing acts to maintain high nutrient-rich forage and increases ungulate carrying capacity (McNaughton 1988, 1990; McNaughton, Banyikwa, and McNaughton 1997).

The factors responsible for causing hot spots are not known. Underlying soil differences cannot be implicated because total soil nutrient concentrations are not different between hot spots and adjacent control areas (McNaughton 1988). Several plausible mechanisms exist. One is that localized rainfall events create concentrated foraging areas by stimulating primary production, after which the high-density herds essentially fertilize large patches through urine and dung deposition, increasing nutrient mineralization and forage quality. A second hypothesis is that hot spots occur on old abandoned termite colonies. As discussed previously, termites change soil nutrient availability and increase forage quality in a way that could remain long after the colony disbands. A third hypothesis is that hot spots represent areas of historical and intense human use, especially behaviors of nomadic cattle herders of the Maasai tribe.

Only the third hypothesis has been adequately tested, with some support, although not in the Serengeti ecosystem. Abandoned cattle bomas create small areas of highly concentrated soil nutrients and forage with low C:N ratios that establish as long-term (> 40 years), grass-filled glades (Augustine 2003). These areas are preferentially used by ungulates and may potentially function as nutrient- and forage-rich hot spots in a new, stable state. The maintenance of nutrient-rich glades by the feeding behavior of ungulates was also identified in arid Kenyan grasslands; herbivores imported nutrients from surrounding woodlands to nutrient-rich glades composed of high-quality, grazing-tolerant grasses (Augustine, McNaughton, and Frank 2003). Calcium, nitrogen, and phosphorus were also at elevated levels in glades; phosphorus, in particular, was at levels high enough to support lactating livestock in the glade but below those levels in the surrounding woodlands (Augustine 2003). The connection between human use and hot spots has not been addressed in Serengeti, and the development of hot spots from abandoned bomas provides but one hypothetical mechanism for their occurrence.

Interactions of Fire, Climate, and Grazing on Vegetation Primary Production

A conceptual model by Osterheld et al. (1999) suggests that the relative importance of fire, climate, and grazing on primary productivity in savanna grassland ecosystems changes across a range of mean annual precipitation (fig. 5.9). At low rainfall, between 200 and 450 mm, interannual climate fluctuations have the greatest impact on production, while herbivore consumption rates and fire frequency are low. Between 450 and 700 mm precipitation, the importance of climate variation decreases, grazing still consumes a relatively small proportion of production, while fire frequency increases in importance but has mostly negative effects. Above 700 mm precipitation, interannual fluctuations in climate are relatively small compared to the effects of fire and grazing. Fire frequency is high and can increase productivity up to five times the mean. Grazing is substantial and can have beneficial effects because of compensatory regrowth. Interannual climate fluctuations can interact with fire and grazing, modifying their importance; this was observed in arid grasslands in Kenya, where overcompensation of primary production following grazing occurred during a wet year but not a dry year (Augustine 2002).

CONCLUSIONS

In summary, the heterogeneity of major vegetation types corresponded to the environmental gradient (e.g., rainfall) in a predictable manner, and the spatial scale at which variables expressed their heterogeneity closely matched the relationships depicted in fig. 5.1. However, a composite measure of heterogeneity demonstrated a significant lack of spatial consistency in heterogeneity across Serengeti grasslands. Regions were composed of adjacent sites that were often more dissimilar than distant sites, even those separated by over 100 km. Important abiotic sources of heterogeneity identified in the Serengeti are climate, fire, and geology, while ungulates (browsers and grazers), vegetation, termites, and humans are important sources of biotic heterogeneity. The agents of heterogeneity are dynamic in time and space and form a complex web of interactions (fig. 5.12). In the last section we attempted to represent some of that complexity by drawing on three examples in which multiple agents interact to affect heterogeneity.

To conclude, we highlight obvious gaps missing from this chapter and in general from studies of heterogeneity across the Serengeti ecosystem. In particular, we have identified four areas that, if elucidated through future research, would greatly enhance the understanding of heterogeneity

Agents of heterogeneity

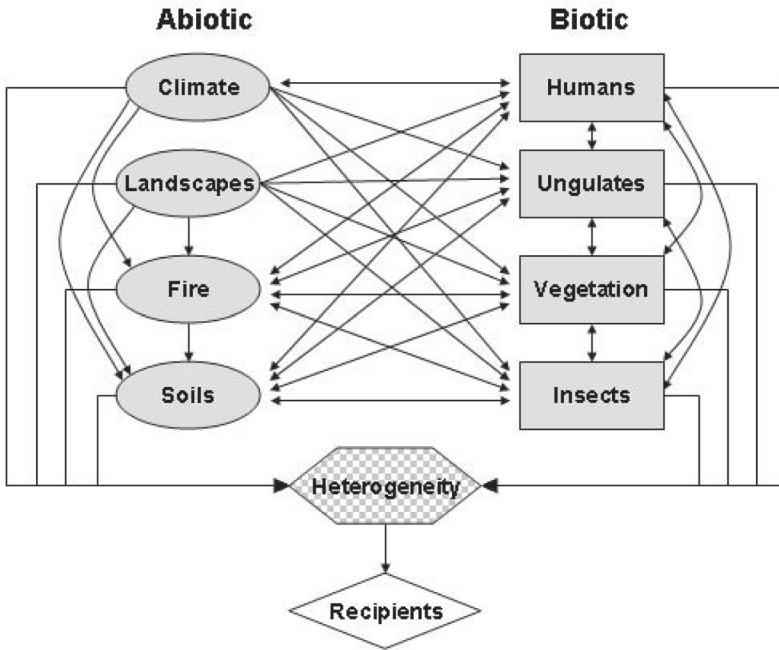


Fig. 5.12 Schematic depicting potential interactions among abiotic and biotic agents of heterogeneity in Serengeti National Park (substrate, controllers, and response not shown). Landscapes = landforms, kopjes, catenas, hills, mountains; ungulates = browsers and grazers; insects = especially termites, dung beetles, tsetse flies; vegetation = herbaceous and woody vegetation; soils = parent material and fertility; recipients include many of the biotic agents listed here so that organisms can modify the ecosystem heterogeneity in the way to which they themselves respond (i.e., positive/negative feedback loops). In these instances, controllers, substrates, and other agents modify the effects of the positive/negative feedback loops, so the system remains stable.

in Serengeti. First, maps of soil (de Wit 1978, Jager 1982), landscape (Gereshiem 1974), and vegetation (Herlocker 1976) of Serengeti reveal considerable heterogeneity on their own. However, interactions among vegetation, soils, and landscape features across the ecosystem have not been considered. An attempt to explore spatial associations between soils, landscapes, and vegetation would provide a decent first approximation of the possibility that their interactions promote emergent forms of heterogeneity. Future work could include hydrological and land-systems models that incorporate feedbacks among biotic and abiotic components.

Second, the movements and behaviors of enormous herds of migratory ungulates are central and defining characteristics of Serengeti. However, an attempt to understand the causes and consequences of spatial and tempo-

ral variation in ungulate migration patterns has not been made. This is a daunting, if not overwhelming, task and will likely take a large collaboration of scientists to study the subject. A recent investigation by Thirgood et al. (2004) provided insight into the complexity of wildebeest migratory patterns. However, understanding the complexity of their movements and the potential to study their behavior as a self-organized, complex system represents one of the most compelling topics facing Serengeti researchers.

Third, as previously discussed, hot spots are key landscape features that provide sustained production of high-quality forage for resident ungulates. While their function is well known, little is known about how they are generated, where they occur, and how long they occupy the landscape. Understanding the spatial and temporal distribution of hot spots may help reveal the factors responsible for their generation and maintenance. The park would benefit greatly from a project to map and monitor hot spots, ungulate densities, and the properties of associated vegetation over time. Such a project would enhance the understanding of ecosystem functioning and enable conservationists and managers to better safeguard natural patterns of heterogeneity that sustain populations of resident herbivores.

Finally, insects, especially termites and dung beetles, have received glaringly little attention in Serengeti. Except for Folse (1982) and the mention of termite structures by those researchers studying plant diversity, information on the distribution, abundance, and effect of insects on ecological processes are all but absent from the Serengeti literature. In similar savanna ecosystems, insects account for a large proportion of animal biomass, and by comparison are likely responsible for the decomposition and redistribution of huge amounts of vegetation biomass and nutrients in Serengeti.

The consideration of these issues imposes a new layer of complexity to our understanding of the Serengeti ecosystems and savannas in general. However, expanding research efforts to incorporate these topics may reveal mechanisms that contribute to the dynamics and diversity that make the Serengeti one of the most singular and cherished ecosystems on earth.

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