

## **RANGELAND COMMUNITIES: STRUCTURE, FUNCTION, AND CLASSIFICATION**

**Kurt O. Reinhart**

*United States Department of Agriculture- Agricultural Research Service, Fort Keogh Livestock and Range Research Laboratory, USA*

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### **Summary**

Determining the vegetational attributes of rangelands is critical to their management. Yet incorporating vegetation structure, function, and classification into a single chapter is an ambitious goal and an attempt to blur the boundaries between classical community ecology that characterize patterns and ecosystem ecology which describe processes. These two disciplines are often non-overlapping and in some respects represent an evolution in research foci from classifying system composition to describing its function with or without regard to its composition. A narrative repeated throughout this chapter; however, is that scientists often do not strictly think about one aspect of vegetation independent of the others and instead merge concepts. This chapter will touch the surface of many topics (i.e. structure, function, life-history, etc.) and devotees are

encouraged to seek additional reading dedicated to these individual topics. These topics are mentioned to the extent that they are relevant to the classification of plant communities. Additionally, this chapter will discuss the linkage between composition and structure. The function of vegetation is also presented as part of the ecosystem concept and developed especially as it relates to classifying species. This section on function will be linked to the previous section with discussion on the linkage between structure and function while touching on the more controversial link between composition (i.e. species diversity) and function. Then vegetation classification and classification systems in general and in the specific context of rangelands will be presented revealing a comparable evolution from emphasis on composition to function. The strengths and weaknesses of various classification systems are discussed.

## **1. Vegetation Composition, Structure, and Life-History**

Many descriptions of vegetation include descriptions of species composition (and diversity), plant structure (and physiognomy), and life-history (i.e. development) which will be discussed in this subsection. Additional descriptions include process oriented descriptions relating to the function of the community/ecosystem like nutrient cycling and productivity which are discussed in Section 2. Lastly, they may also include descriptions of species patterns and development over time (i.e. succession) which are discussed in Section 3.

The most desired classification schemes are often those that characterize the community or ecosystem that have a clear understanding of the system and its management by grouping species, to the degree possible, into classes of similar characteristics or behaviors. Some classification systems in use integrate more than one classification scheme instead of maintaining a pure classification system that focuses exclusively on one of these topics. One dimensional descriptions of vegetation are likely an inaccurate portrayal of reality because individual species are potentially plastic in form and function and occur across multiple communities and ecosystems which are dynamic over time and space.

### **1.1. Composition**

Vegetation can be classified in many different ways. A purely taxonomic perspective would emphasize the phylogenetic relatedness of species at a site or habitat. However, ecologists are often not very satisfied with classifications solely focused on characterizing phylogenetic relationships. Additional descriptions are often desired (e.g. plant structure, species composition, life-history, function, etc.). Compositional descriptions are one way to describe a system and often include estimates of the dominance, commonness, and rarity of species. Compositional estimates for rangelands often focus on biomass descriptions (e.g. grams per meter, kilograms per hectare, etc.) instead of estimates like percent cover which do not necessarily have a clear relationship with biomass/forage production. System productivity is both a compositional, structural, and functional attribute. A variety of techniques ranging from counts, quadrats/plots (may be nested or not to account for vegetation strata), point quadrats, and transects can be used to quantify plant density, frequency, cover, and biomass (i.e. dry weight). The Braun-Blanquet method is another widely used method to

quantify the vegetation (produces discrete quantitative data also referred to as categorical data). This method involves identifying a specific area of study, identifying all species present in the study area, and then assigning a code based on its relative abundance (e.g. 0: species not present, 1: species <5% of total, 2: species= 5-10% of total, etc.). Another type of compositional description is the mapping of vegetation. Because plant communities generally represent a diversity of plant species, they must be classified and then mapped. Typically, most vegetation maps rely on some degree of vegetation classification. Thus, this is discussed further in Section 3. Because vegetation varies seasonally and yearly (e.g. total production, abundance of annuals vs. perennials, presence of early season vs. late season plants, etc.), multiple measurements over time (in and among years) and space may be necessary to account for natural patterns of variation. The most appropriate method is likely to depend on the type of vegetation being sampled, intended sampling effort, type of data desired, etc.

Species diversity or the number of species per unit area, referred to as species richness, is often used to describe the composition of plant communities. Because not all species occur at equal numbers, other metrics of diversity are considered such as: species evenness (the relative abundance of species with some being dominant and others rare) and species diversity (a composite descriptor of species richness and evenness). Species diversity accounts for both the species richness and their evenness/commonness. Some confusion is possible because estimates of species richness are often referred to as diversity. A number of metrics of evenness (e.g. Shannon evenness, etc.) and diversity (e.g. Shannon-Weiner index, Inverse Simpson's index, Pielou's index, etc.) exist. Three types of diversity are often discussed that vary with scale. Alpha diversity generally describes the number of species for an ecosystem. Beta diversity compares the diversity of species between ecosystems. Gamma diversity is a measure of overall diversity of ecosystems in a region.

Quantifying species diversity in a meaningful way can be tricky. Although absolute values are useful, they can be misleading. For example, the sampling effort used to quantify alpha diversity will affect this measure of diversity since additional sampling (or surveys at larger spatial scales) often yields additional species. A range of analytical procedures are available including accumulation curves and rarefaction methods to account for sampling intensity. Estimates of species diversity may be further limited by not accounting for the attributes of species. For example, most scientists would agree that a system with three species consisting of one early season grass ( $C_3$  photosynthetic pathway), one late-season grass ( $C_4$ ), and a nitrogen fixing forb (legume;  $C_3$ ) is more diverse than a system with eight early season grass species. This example highlights the value of incorporating multiple complementary approaches including assessments of composition, plant structure, life history, and function.

The earth's biomes, largest categories of plant communities, display remarkable similarity and convergence in structure and function (i.e. physiognomy) regardless of taxonomic similarity. Thus, descriptions of the ecological traits of species in a community are often more revealing about the community than simple tabulations of species without any knowledge of their attributes. Ecological traits typically relate to the form, life-history, and function of species. In the next two subsections, will vegetation form and life-history will be discussed and in the next section will discuss function.

## 1.2. Structure

Plant communities display a diverse range of three-dimensional structures. Vegetation structure (or morphotypes, life-forms, etc.) relate to the structural attributes of plants. One of the most historically significant systems used to describe plant structure is the Raunkiaer system established by Christen C. Raunkiaer. This system describes the morphological attributes of plants based upon the position of their apical meristems in relation to the soil surface and describes five types of vegetation: phanerophytes (trees), chamaephytes (shrubs), hemicryptophytes (all plants with overwintering buds at the soil surface), cryptophytes (buds below ground), and therophytes (annuals where the bud survives in the seed). Although this system appears to describe plant structure, it also has relevance to underlying functions—winter survival and frost resistance. The principle limit of this system, and other related systems that focus on the variation of a single trait, is that very different plants may end up in the same category. For example, deciduous and evergreen trees are in the same category. There are inherent limits to any classification system that relies upon a single criterion to make meaningful groupings while acknowledging that vegetation occurs across a diverse range of environments. Other attempts to categorize plants by their structures have considered plant size, leaf size/shape/texture, permanence of canopy, root morphology, branching patterns, profile diagrams, etc.. An emerging property of these is that variation in structural morphology is often linked to function. Thus, form and function are often closely associated. However as noted in Section 2, plants are often plastic and can alter their structure and function with changes in the environment.

Probably the most widely used grouping of vegetation, does not rely upon single traits. The most accepted structural classification describes vegetation as follows: trees (and their types), vines, shrubs, dwarf shrubs, creepers, forbs maintaining basal rosettes, tall forbs, grasses (and possibly a few types), geophytes, epiphytes, leaf and stem succulents, bryophytes, and lichens. Like most attempts to group species these groupings (or some derivation) are not always distinct. Some species may have morphological traits causing them to associate with more than one group. Although this can complicate the utility of this system, it has proven of great practical value and is widely used. Often, this classification system is merged with life-history (annual vs. perennial) and functional traits (e.g. nitrogen fixer, C<sub>3</sub> vs. C<sub>4</sub> photosynthetic pathways, etc.).

## 1.3. Life-History Traits

The life-history traits of plants concern the schedule of birth, growth, reproduction, and mortality of individual and populations of species. They are not purely related to either plant structure or function but are an additional way that ecologists have classified vegetation into meaningful groups. Life-history traits relate to descriptions of life spans of plant species (e.g. annual, biennial, or [short or long lived] perennial). For example, annual plants are often most abundant in early secondary succession (e.g. following agricultural abandonment) and in ecosystems with a great deal of disturbance. Life-history traits also concern the reproductive cycles as either a single event or multiple events. These descriptions are probably best applied in addition to other descriptions of vegetation (i.e. composition, structure, and function).

Life-history traits are often related to ecological trade-offs. An ecological trade-off is assumed to exist when a constraint exists that prevents a species from attaining multiple optimal traits simultaneously. For example, a trade-off is known to exist between seed size vs. seed number. In this case, a limited amount of resources are available to allocate towards reproduction so a trade-off exists in producing either a lot of small seeds or a few large seeds. Intermediate quantities and sizes can also be achieved. However, producing a lot of large seeds is not energetically (or structurally) feasible. Although mathematical models often predict that only a single life-history is optimal for a given environment, species making up a natural community tend to reflect diverse life-histories helping illustrate the temporal and spatial complexity of natural systems.

Robert MacArthur and colleagues are often attributed with developing the foundations of life-history evolution. They predicted that species vary in traits associated with either r- or K-selection. The terms “r” and “K” refer to intrinsic rate of population growth (i.e. rate of increase) and carrying capacity (i.e. saturation density) respectively in the logistic model of population growth. Conceptually, r-selected species are ones with great ability to colonize and grow. They are often described as weedy species. However, they are much less capable of competing with other species while K-selected species are thought to excel at resource competition. Although K-selected species are predicted to excel at resource competition r-selected species may persist because resource competition is only one interaction affecting populations. Other interspecific species interactions (i.e. multi-species interactions) exist in addition to resource competition that promote species coexistence and prevent a K-selected species from completely displacing r-selected species.

Philip Grime extended the r- and K-selection theory by proposing that life histories are influenced primarily by three traits: colonizing ability (R selection, for ruderal “weedy” species), competitive ability (C selection), and stress tolerance (S selection). He assumes that there are trade-offs for each of these three syndromes. In some systems, species may seem to easily fit the C, S, R scheme. However, these three classifications are conceptual in nature and not easy to quantify. So although widely cited, the CSR model has generated considerable controversy resulting largely because of an inability to quantify and characterize the three critical traits. An extension of the CSR model was created by Mark Westoby and is referred to as the leaf-height-seed (LHS) scheme. Westoby’s method is conceptually like Grime’s but is more quantifiable. The LHS scheme measures specific leaf area (leaf), canopy height at maturity, and seed mass.

Considering facets of the composition, structure, and life-history reveal a great deal of information about plant communities.

#### **1.4. Structure and Composition Linkage**

In many cases, some basic knowledge about the composition of a community will reveal a great deal about the physical structure of the plant community. This is because many genera of plants have cosmopolitan distributions and species of the same genus often have similar general morphology or growth forms (i.e. vertical structures, degree of woodiness, etc.). Despite the characteristics that distinguish individual species of a genus, closely related taxa are likely to share a common growth form. This is useful to

know because we can piece together a general understanding about the plant community structure by knowing the identity of the most common species (by biomass) of a system. We may not be familiar with the specific species because they are from a plant community and/or place with which we are unfamiliar. However, we may be able to deduce the community structure by relating this unseen plant community to regional communities with related species familiar to us. Specifically, imagine that the community is dominated by genera of grasses or woody plants (e.g. oaks, pines, maples, shrub genera, etc.). Having this level of knowledge will allow us to identify regional communities with similar taxa and will help reveal the general structure of the plant community (grassland, shrubland, forest, etc.). In Section 3, we will discuss how the most general classification of vegetation describing its physiognomy relates to major environmental drivers of the system. With this added knowledge, either direct or indirect knowledge (i.e. composition of dominant species) about the growth form of the plants will reveal the general ecosystem/biome which will also reveal the key features of the environment shaping the vegetation. This is because of the link between structure and function elaborated in the next section.

## **2. Ecosystem Function**

Understanding ecosystem function requires an accounting of the inputs and outputs of energy and resources for a system. The term ecosystem was first described by A. G. Tansley; however, Raymond Lindman is often credited with the modern definition. He proposed that energy flows through several trophic levels. Trophic levels makeup food webs where primary producers, like plants, convert nonliving matter (i.e. gases, liquids, etc.) into living tissue. Consumers then digest this material and in turn are preyed on by carnivores. The energy flow in an ecosystem moves through several trophic levels. At each transition materials are transformed from one state to another.

A key component of ecosystem function is the supply of ecosystem services. Critical ecosystem services include the production of clean water and air, decomposition of waste products, nutrient cycling, etc. Ecosystem services are essential because they maintain humankind. Ecosystem services are often broken down into five categories: 1) provisioning (i.e. producing food and water); 2) regulating (controlling climate); 3) supporting (nutrient cycling); 4) cultural (historical significance, inspiration, recreation, etc.); and 5) preserving (maintaining biological and genetic diversity to protect against and enable [e.g. new medicines are often first identified by assaying living organisms] the unforeseeable).

Ecosystem ecologists often focus on functional attributes of systems like quantifying the carbon budget of a system and more specifically accounting for its flux (i.e. total carbon assimilation and production from respiration) of the system without regard to species-level effects. Accounting for species-level effects may require a minutia of information. For example, having a general understanding of soil respiration and how it is regulated may be sufficient instead of accounting for the contribution of each soil microbe, arthropod species, and root of individual plant species in the soil.

Understanding ecosystem function is also important for assessing rangeland health. Rangeland health has been defined as the degree to which the integrity of the soil and

ecological processes of rangeland ecosystems are sustained (Committee on Rangeland Classification 1994). This is discussed further near the end of Section 4.3. Some of the most recent advances in classification systems include a much more significant focus on assessing range health through key descriptions of the system that tie directly back to understanding and quantifying ecosystem function.

Ecosystem function is essentially the net outcome of all the functions of species in a system. This is not exclusive to plants, although they are a major driver (i.e. primary producers) of the system, but includes organisms ranging from microbes to large animals. Related to this and the previous sections on classifying vegetation based on composition, structure, and life-history; plants are also grouped based on their functions. Functional groups or adaptive syndromes are another means to group species. A critical assumption is that plant traits are directly related to the physical environment of the plant. Ecologists often assume that these traits are adaptive in the sense that they increase the overall fitness of the species (i.e. adaptive value).

The most common functional groups are single character functional groups. To some extent, all plants share a common physiology since they have a common evolutionary ancestry. Although there is considerable physiological similarity among plants, they also display considerable functional variation. For example, plants are described by their photosynthetic pathways ( $C_3$ ,  $C_4$ , and Crassulacean Acid Metabolism [CAM]), ability to fix nitrogen, etc.. Distinctions in photosynthetic pathway are prominent largely because they are clear cut with species clearly falling into one of the three classes. A number of studies have shown that  $C_4$  and CAM plants differ in their ability to withstand drought and temperature. Biogeographical patterns reveal that  $C_4$  plants are most prominent in warm and seasonally dry environments and CAM plants are often in warm and dry environments. Classification systems often incorporate descriptions of life-history and structural characters. For example, the description of a plant as an early season ( $C_3$ ) perennial grass combines a description of its function, structure, and life-history. Other physiological functions that may be useful to incorporate into a classification system are: drought resistance, soil nutrient requirements, temperature susceptibility, etc.. However, many of these functional attributes are plastic, and plants will modify their morphology (root/shoot ratios, position of leaves in the canopy, leaf size and thickness, etc.) and physiological processes to compensate for changes in water, temperature, and light. Plant races or ecotypes also exist and reveal variation in functional attributes among populations of a species. This has been noted for plant species that occur across a broad elevation or latitudinal gradient. Some of these differences in plant phenotype (i.e. physical and physiological traits) are genetically based. For example, phenotypic plasticity occurs when a plant with a specific genotype changes its phenotype in response to environmental signals.

Although widely used, the value of functional groups is debated. At the core of the debate is whether functional groups provide sufficient information to describe ecosystem processes. An inherent assumption to using functional groups is that all species in a group are functionally redundant. This is not necessarily true and may oversimplify the complexity that distinguishes species. The impact of (local) extinction of an individual species depends on the uniqueness of its functions and how much other species can compensate for the loss and buffer the entire system. Some functions may

be more redundant across species than others. Determining how much species-level variation to account for to adequately describe the functioning of ecosystems will continue to be debated.

A comparison of biomes reveals that plants with varied phylogenetic relatedness tend to have similar functional traits. For example, cacti in the New World (Americas) have an entirely different ancestry from the structurally/functionally similar succulents of the Old World (Africa). Plants in similar environments tend to have converged upon similar structures and functions regardless of their degree of relatedness. Thus, the environment is a major driver selecting for specific functional traits that ultimately affect the fitness (i.e. survival and reproduction) of species in individual environments.

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### Biographical Sketch

**Kurt O. Reinhart** - an ecologist working for the United States Department of Agriculture-Agricultural Research Service at the Fort Keogh Livestock and Range Research Laboratory in Miles City, Montana, USA. His current research program focuses on the importance of plant-microbial interactions in maintaining grassland diversity, productivity, and stability. Current research suggests that microbes are critical for maintaining plant species, plant communities, resilience, and ecosystem function (e.g. nutrient cycling, soil stability, etc.). His research program explores how unseen microbes affect plant communities (e.g. composition, productivity, vulnerability to invasion, soil structure, etc.). He received Ph.D. from The University of Montana in 2003 and was a post-doctoral research associate at Indiana University, Bloomington until 2007. He worked in diverse systems ranging from salt marshes, forest

epiphytes, scrublands, grasslands, and forests. His research experience is equally broad and spans topics relating to plant community ecology, plant ecophysiology, plant-microbe interactions, invasion biology, etc.. His most notable research integrates plant-microbial interactions with invasion ecology.

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