The Intersection of Ecosystem and Biodiversity Concerns in the Management of Rangelands

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Abstract

Maintenance of ecological functions and disturbance regimes within ecosystems is as important as preserving species populations or their genetic structure, biotic communities, and landscapes. There is considerable dispute as to how species diversity influences productivity and stability of various ecosystem structural and dynamic attributes. Some view each and every species as making an incremental contribution to these features. Others assume that some redundancy exists. Addition or loss of species can be anecdotally shown to influence ecosystems in proportion to the role such organisms have in altering microclimate, capturing energy, cycling nutrients, and serving as food and habitat for other organisms. Subtle but essential interactions are easy to overlook, however. We should try to keep all the parts until more definitive research is available on this topic. Sustainable development will require balancing resource use with maintenance of our natural legacies. Ecosystem perspectives must contribute to decisions on where the balance exists.

INTRODUCTION

Maintenance of ecological functions, processes, and disturbance regimes is as important as preserving species, their populations, genetic structure, biotic communities, and landscapes. Hence ecosystem-level processes, services, and disturbances must be considered within the arena of biodiversity concerns.

In the following, we will define ecosystems, illustrate ecosystem structure, function, processes, and disturbance regimes, and consider whether equilibrium and integrity exist. We will also review how diversity relates to stability and productivity. We will then conclude with recommendations to land managers interested in this topic and researchers who wish to help them.

ECOSYSTEM DEFINED

An ecosystem is defined as the biological community plus the physical environment with which it interacts. One can view ecosystems as either abstractions emphasizing processes such as energy flow, biogeochemical cycles, hydrological relationships, etc., or as bounded, concrete places on the earth's surface. Ecosystems may be as small as a single plant with its associated soil, atmosphere, and fauna or as large as a watershed or a geographic region. While it is comparatively easy to define a watershed and the hydrological cycle of that area, it is impossible to capture completely all of the interactions between the atmosphere, biota, soils, etc. A test of this statement is the challenge to try to map just one part of an ecosystem, e.g., the nitrogen cycle (Allen and Hoekstra 1992).

Ecosystems remained abstractions as long as land management was focused on goods rather than services or processes (Table 1). Now that management perspectives have shifted from goods only to include services and processes (Kessler et al. 1992), it is essential that we determine what functions are occurring and at what rates in order to gauge the integrity of an ecosystem (Rapport 1989). In addition, it is necessary to understand how that ecosystem contributes as a source or sink of energy and materials within its larger region and even in the global context.

ECOSYSTEM FUNCTIONS

Ecosystem functions translate into vital services (Table 1) to human society such as water conservation, balance of atmospheric gases, and waste degradation. Society is beginning to understand the need to sustain intact and productive wildlands, not just for their extractable goods, but also as life support systems.

TABLE 1. VALUES OF ECOSYSTEMS

Goods (Materials)
    Foods
    Fibers
    Fuels
    Medicines
    Building Materials
    Industrial Products
    Genetic Resources
    Aesthetic, Cultural, Spiritual Renewal

Services (Life Support Systems)
    Maintenance of Atmosphere and Hydrosphere
    Amelioration of Climate
    Origin and Maintenance of Soils (and their
      buffering capacity)
    Absorption and Degradation of Wastes
    Natural Control of Pathogenic and Parasitic
      Organisms

Processes
    Production of Organic Matter
    Decomposition of Organic Matter
    Nutrient Cycling
    Grazing Regime
    Fire Regime
    Hydrologic Regime
      Infiltration
      Runoff
      Evapotranspiration
    Soil Erosion Regime

A large segment of human society now questions management approaches that simplify ecological systems by concentrating nutrients and energy into efficient production of desired goods. The full array of values (goods, services, processes) of wildlands may be compromised by ecological simplification. Ecosystem structure and function, rates of ecosystem processes and disturbance regimes, and their stability are influenced by biotic diversity from the genetic to landscape levels (Solbrig 1991a). The quantitative interrelationships are, however, unknown for the most part and therefore the subject of considerable controversy (Pimm 1991).

ECOSYSTEM PROCESSES

Examples of major ecosystem processes are flow of energy, cycling of nutrients, fire, soil erosion, and hydrological regimes. Climate may be the principal driver of these processes, but interactions between land use and biotic influences and their feedbacks may markedly alter these processes. Abundance of particular species can have disproportionately large effects on these processes. For instance, Vitousek (1990) has shown how the invasion of a single species of nitrogen-fixing tree into Hawaii is beginning to alter everything else about those ecosystems. The invasion of cheatgrass *(Bromus tectorum)* into the Great Basin is another example of how ecosystem-wide alterations can occur with the addition of only one exotic species (Billings 1990). Hobbs and Huenneke (1992) review this topic more generally, illustrating how maximal diversity is usually found at intermediate frequencies of disturbance. Thus, if managers wish to maintain such diversity and limit local extinctions and invasions, more than passive protection is needed.

Dramatic changes in entire ecosystems are generally slow. Because we can rarely observe impacts species by species, ecologists have often resorted to concepts such as guilds, functional groups, leagues, and minimal structure, while recognizing the necessity to consider keystone species, critical link species, and exotic species.

It is impossible to prevent all environmental degradation, species extinctions, and species invasions. The human population of the planet is already too large, especially in view of the increasing demand for goods and services as populations in less developed parts of the world raise their expectations for living standards. In addition, the extreme mobility of humans and their penchant for transporting organisms with them makes it impossible to diminish further movement of organisms to new locales. The establishment of non-native species will generally relate to the degree of landscape fragmentation and variable disturbance (Hobbs and Huenneke 1992) and have impacts in proportion to the adventives' roles at the ecosystem level (Vitousek 1990).

Because of the inevitability of both environmental and biotic change, it is essential that we alter our unrealistic focus on the past, particularly the supposed equilibrium condition of the pristine. We will not go that way again (Allen and Hoekstra 1992, Hobbs and Huenneke 1992). We need to shift focus from the pristine and equilibrium condition to nonequilibrium or nonsteady state ecosystems in which future pathways of change may be different, stochastic, and even chaotic. Given that ecosystems do not behave as equilibrium conceptual models predict, the question becomes, can we maintain their biological and ecological integrity?

ECOSYSTEM INTEGRITY

Some prefer to talk of ecosystem "health" (Rapport 1989). We contend that this is not a good metaphor because it leads to superorganismic thinking. We prefer the expression "ecological integrity." Establishment of standards for ecosystem integrity will revolutionize the management of wildlands because we will be forced to confront the ethical questions of how humans fit with nature (Grumbine 1992).[1]

There is no agreement about what is meant by ecological integrity. Cairns (1977) defines biological integrity as "the

[1]See West, this volume.

maintenance of community structure and function characteristics of a particular locale deemed satisfactory to society." West (1993) defined ecosystem integrity as preservation of the remaining soil profile, plus reasonable levels of the critical ecosystem functions of energy flow and nutrient cycling such that human society maintains options, mainly for food production.

Salwasser (1994) defines ecosystem integrity as "possession of a full set of natural parts and processes in good working order." Can ecosystem integrity be defined through purely biological data or need environmental factors and their interactions with biota be monitored? In order to answer that question, it is necessary to review briefly current theories of community-ecosystem interactions.

THEORIES OF COMMUNITY–ECOSYSTEM INTERACTION

DIVERSITY/STABILITY

For diversity, we here mean taxonomic richness of the biotic community at the alpha level.[2] We are thinking of stability in this context as maintenance of rates of function (e.g., net primary production, nutrient cycling).

RIVET HYPOTHESIS

Most ecologists have held to the notion that increased diversity results in increased stability. Ehrlich and Ehrlich (1981) called this notion the "rivet" hypothesis. This hypothesis assumes that each species plays an incrementally important role (like that of rivets in holding an airplane together). Thus, after the loss of a certain set of species, a threshold is crossed and rapid degradative change occurs (the airplane crashes). This is really a restatement of Aldo Leopold's first rule of ecological tinkering—save all the pieces. The assumption that all species need to be retained is at the core of Grumbine's (1994) view of ecosystem management.

REDUNDANCY

Another approach, the theory of structural and functional redundancy, conceptualizes communities as composed of a few structural and functional groups, each of which is composed of several ecologically equivalent species. In such communities, some species may be lost with little or no effect on ecosystem processes (Walker 1992). Thus, redundancy at the species level can be thought of as "insurance" or "backup" because each species within the group is functionally equivalent.

Which is the more reliable model?

Common sense favors the rivet hypothesis. The logic used is that although each of the species within a group can tolerate only a limited range of climatic and biotic conditions, the tolerances of each species probably differ at least somewhat from those of all other species within the group. The logic of those favoring redundancy is that with several species in each structural and functional group, those structural and

functional features are more likely to persist under global environmental change. However, Odum (1992) points out that maybe the backup components are not as efficient as the primary ones.

The modeling efforts of May (1973) showed no increase in stability with increased species diversity and food web complexity. May's definition of stability was, however, quite restrictive. Peters (1991) reviews this topic, including the modeling, and concludes that it is hopelessly confused.

Very little direct experimental data yet exist to favor one theory over the other (Simpson 1988, Solbrig 1991a, Chapin et al. 1992). A lot of research on this topic is now under way, however (Anon. 1993, Baskin 1994). Tilman and Downing (1994) reexamined some data from fertilized Minnesota grassland recovering from drought and concluded that more diverse grassland plots showed greater resistance to and recovered more fully from drought. Each additional species lost from their grasslands had a progressively greater impact on drought resistance. Further long-term detailed observations of ecosystems (Holdgate 1991, Walker 1992, Solbrig 1991b, Frank and McNaughton 1991, Heal et al. 1993) will be required before greater generality can be reached. Until the results of such studies are published for a variety of ecosystems, we are reduced to either logical or historical arguments, a style of research with distinct problems (Peters 1991).

DIVERSITY/PRODUCTIVITY

Earlier workers believed that increased diversity inevitably led to increased productivity, thinking that as more species appeared there were self-augmented appearances of organisms at higher trophic levels. Marshes, however, are systems with low plant species richness but with considerable trophic diversity (complexity of food webs) yet with some of the highest levels of overall productivity. Most ecosystems, however, have species richness higher than that required for efficient biogeochemical and trophic functions (DiCastri 1991). Functional groupings have been proposed as a means of aggregating species having similar effects on ecosystem processes (Walker 1992). The term *functional group* defines a species assemblage in which all of the species perform a certain functional role in the ecosystem. Functional group contrasts with guild, which has come to mean all species using some resource (Simberloff and Dayan 1991). Because we can never determine how each species affects all ecosystem functions, aggregates such as "functional group" may be a practical necessity. In functional groups with more than one species, there is the implication that one or more of the species may be equivalent or redundant. Implicit in this is the assumption that the ecosystem could function equally well with fewer species in that functional group. A species, however, doesn't just fit in one functional group. It may be a critical member in another grouping that wasn't examined. Faber (1991) has introduced the concept of "league," which assembles organisms by their exploitation of or processing in more than one habitat.
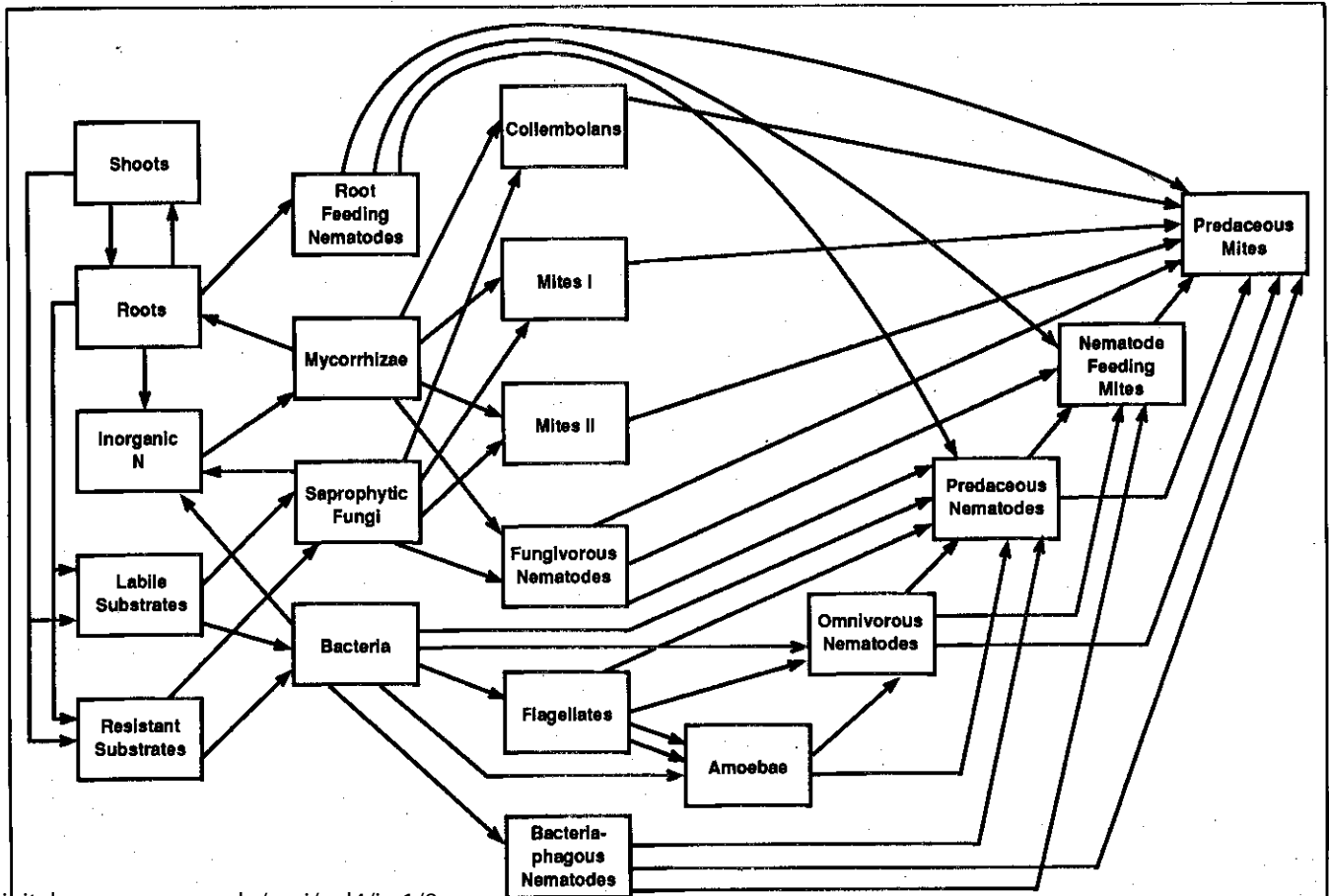
Many examples of the use of functional groups in ecological research come from studies of the biological control of biogeochemical cycles. This is largely because of severe

[2]See Moir and Bonham, this volume.

West and Whitford, Figure 1. The top half of the figure was omitted. Below is the correct and complete figure.
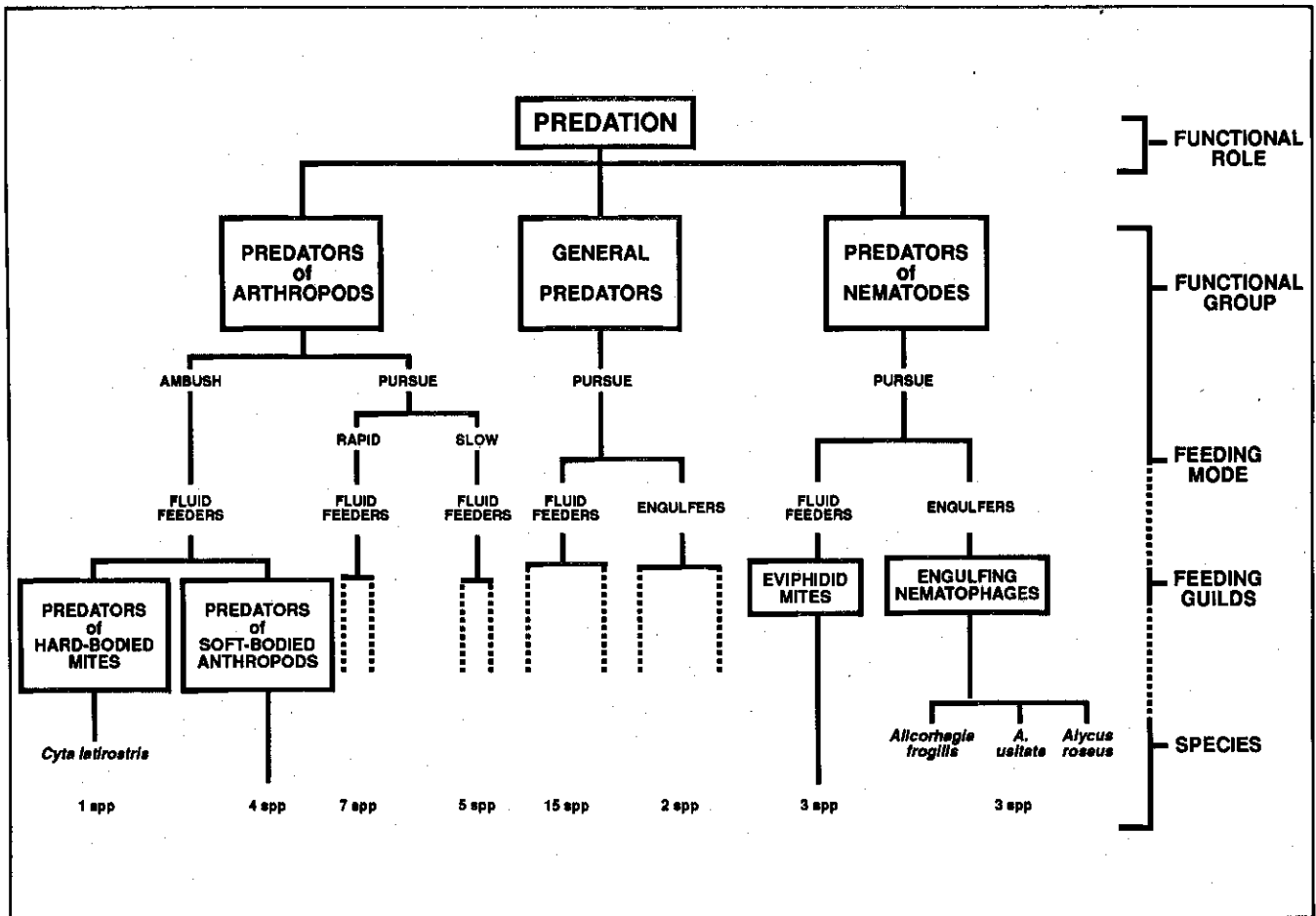
deficiencies in taxonomic determinations of organisms living belowground (Klopatek et al. 1992). Thus, much of the research on belowground processes has of necessity focused on functional groups, and on guilds such as bacterial-feeding nematodes and fungus-feeding mites (Ingham et al. 1986a, b, Parker et al. 1984, Elliot et al. 1988, Whitford and Parker 1989) (Figure 1). These functional groups contain many species and the biogeochemical processes proceed in what appears to be a "normal" fashion in microcosm studies in which the diversity of species in any functional group was greatly reduced (Cole et. al. 1978). Even when a single functional group such as predatory mites was broken down into finer subdivisions, most of the subdivisions remained characterized by multiple species (Elliott et al. 1988), implying that many species within each functional group may be equivalent or redundant.

Anecdotal, historical evidence also appears to support the idea of redundancy in functional groups. For example, while the loss of American chestnut trees and passenger pigeons from the eastern deciduous forests of the United States led to some short-term economic impacts for that small segment of the population that harvested these species for food or fiber, other species filled in the space and drew on the resources that those species once utilized. The end result of those extinctions was that no undesirable long-term changes in total productivity and watershed protection were noticed (Johnson and Mayeaux 1992).

Proponents of the rivet hypothesis would counter that loss of any species is important and forever. The genomes of passenger pigeons cannot be used to improve the world's genetic options via any technology that we now possess (but scenarios like that in Michael Crichton's book *Jurassic Park* may become real some day). Furthermore, devising any structural or functional categories results in arbitrary overgeneralizations that possibly mask the structural and functional uniqueness of any individuals or species populations.

As is the case with the passenger pigeon and chestnut, because we generally lack sufficiently detailed data on the conditions before and at the time of the extinctions, we could be overlooking subtle associated losses or consequences. For example, we have no knowledge of the ecosystem connections of the seven species of lepidopterans that fed exclusively on American chestnut and thus have become extinct (Opler 1977). There were concomitant impacts on the forests besides the chestnut blight, e.g., timber harvesting, air pollution, excessive hunting, livestock grazing (particularly by hogs), etc. These may have uniquely interacted with the loss of the tree and the pigeon.
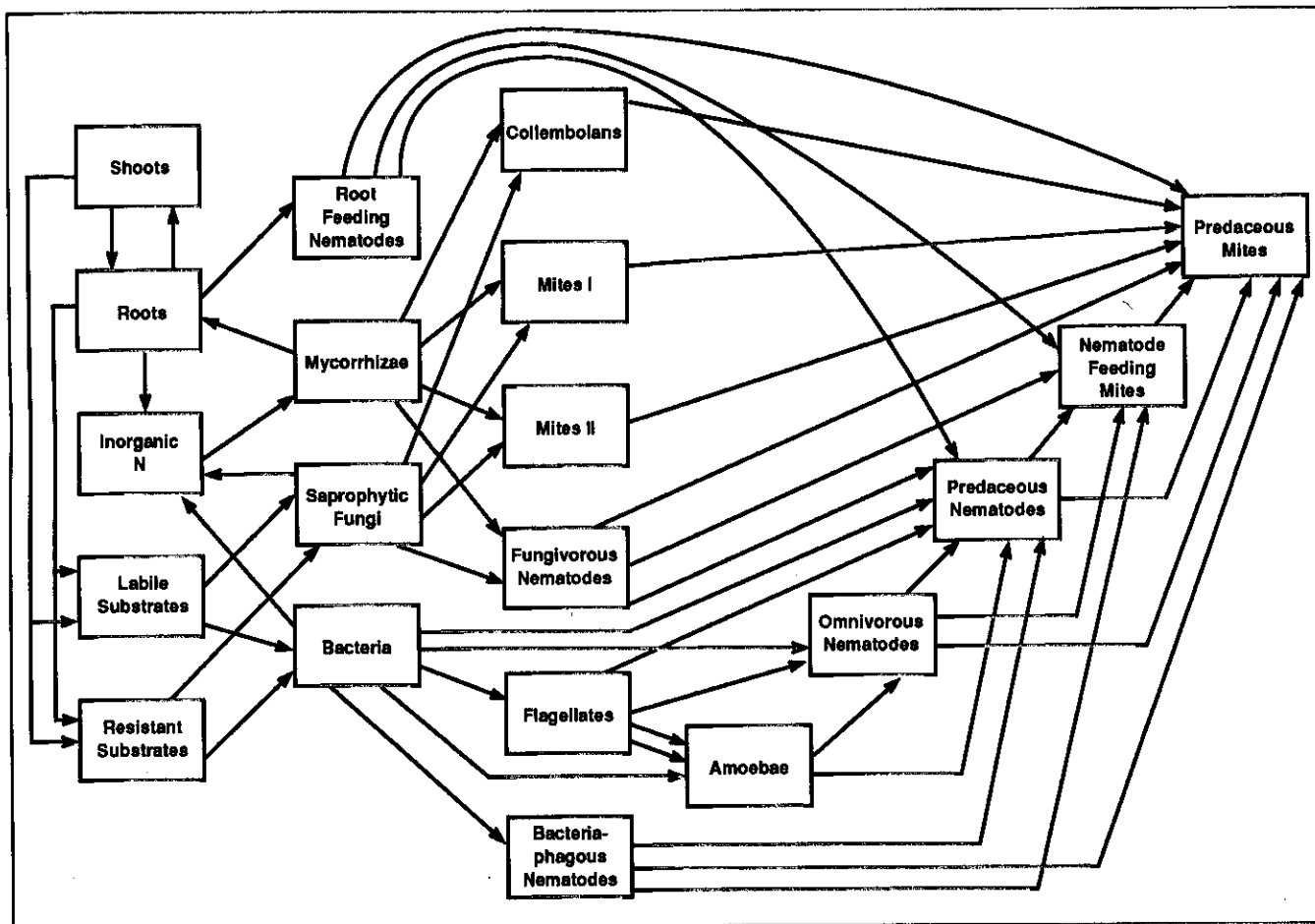

Figure 1. Belowground food webs

ACTIONS NEEDED

Analysis of past incidences of extinctions suffers from inadequately detailed data and lack of replication and control. Studies of only the past will thus never defuse the debate over hypotheses of community-ecosystem interactions. Well-designed experimental studies are needed where they are tractable and ethical. However, most ecosystems are too large and unique to find replicates. Furthermore, control and manipulation of just one factor at a time is unreasonable (Eberhardt and Thomas 1991). Thus, what is currently needed is to combine management and research in an approach called adaptive resource management (Walters 1986, Allen and Hoekstra 1992) and monitor some management units closely enough to allow us to see if simplified ones are functionally less desirable than the biotically richer "controls."

All species are not created equal. Some are "drivers" and some are "passengers" (Walker 1992). The extent of change will largely depend upon the tightness of the linkage of major species to others in the food web (Pimm 1991). Considerable effort must be invested in the identification of these major linkages. Until convincingly demonstrated otherwise, Leopold's axiom should prevail—save all the pieces possible.

LIFE FORMS AND ECOSYSTEM ARCHITECTURE

Biological communities are frequently described on the basis of dominant life forms or structural dominants, e.g., bunchgrass steppe, open woodland, thorn scrubland, etc. The life form of such dominant species affects important ecosystem properties and processes. These dominants are the organisms that directly interface with climate and modify microclimates associated with them in their immediate environment (e.g., Pierson and Wight 1991). These are the species that Solbrig (1991c) refers to as "structural" species that by virtue of their size, abundance, and structural features influence the local environment. "Structural" species may have direct influences on ecosystem services such as ground water and stream water. For instance, from a recent study in Great Britain, stem flow water from trees on wooded hillslopes was shown to bypass the soil matrix by rapidly following root channels (macropores), accounting for the major characteristics of stream hydrographs (Crabtree and Trudgill 1985). Vetaas (1992) reviewed the contributions of trees and shrubs in savannas to water and nutrient distribution patterns and on species composition and community diversity. That review points to the importance of these "structural" species in influencing ecosystem properties. Obviously there may be redundancy in species that are the "structural" dominants, e.g., pinyon and juniper in those woodlands. However, the potential importance of such dominants and the frequently overwhelming importance of a single "structural" species in an ecosystem suggests that structural species should be carefully considered with respect to their effects on ecosystem goods, services, and processes.

KEYSTONE SPECIES

Species whose direct or indirect effects on the survival of other species or on ecosystem function is disproportionately large in relation to their abundance are called "keystone" species (Westman 1990). Keystone species fall into three general classes: (1) keystone predators, (2) keystone mutualists, and (3) keystone resource species. Keystone predators are carnivores, herbivores, parasites, or pathogens that allow the maintenance of diversity among competing organisms by reducing the abundance of dominants and thus prevent competitive exclusion. An example of a keystone predator is the wolf in many North American and Eurasian wildlands with abundant ungulates. Keystone mutualists are organisms such as mycorrhizae and honey bees that link the fate of many partner species. Keystone resource species provide resources during bottlenecks of resource availability or chronically low resource availability. A rangeland example would be prickly pear cacti serving as a food resource for animals as diverse as javelina and coyotes, and even cattle during drought. Another example of a resource species is the N-fixing plants in semiarid to arid regions. By definition, there is no redundancy in the critical function of a "keystone" species.

The keystone-species concept has been expanded to include guilds or functional groups of species (Simberloff and Dayan 1991). For example, Brown and Heske (1990), in a long-term experimental study in the Chihuahuan Desert in eastern Arizona, found that without kangaroo rats (*Dipodomys* spp.), there was a significant reduction in shrubs, but a significant increase in grass cover. Investigations by Chew and Whitford (1992) and Hawkins and Nicoletto (1992) have reinforced this view of kangaroo rats as a keystone group.[3]

Another keystone functional group in many subtropical deserts, grasslands, and savannas is subterranean termites. These animals process more than 50 percent of the dead organic matter and herbivore dung in the Chihuahuan Desert, as well as physically modifying the soil and thereby affecting infiltration, water storage, and nutrient cycling. Elimination of termites on experimental plots has resulted in marked changes in species composition and/or productivity of annual forbs, perennial grasses, and shrubs (Whitford 1991).

Given the constraints of the experimental designs in the cases discussed above, it is not possible to say unequivocally that the keystone species in these examples are Merriam's kangaroo rats *(Dipodomys merriami)* and termites *(Gnathamitermes tubiformans)*, despite their relatively high abundance with respect to other potential species in the group. Mills et al. (1993) warn us to use care in defining what we mean by keystone species. Different questions will require different approaches (Allen and Hoekstra 1992). Man could be considered to be the major keystone species in most present contexts (Salwasser and Pfister 1994). Obviously considerable work is necessary to identify keystone species and their effects on ecosystems. These species are of obvious importance to land managers, but there is scant knowledge of them for rangeland ecosystems.

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[3]See Parmenter et al., this volume, for further detail.

EXOTIC AND ALIEN SPECIES

Policies calling for removal of all exotic, alien, or introduced species appear to rest on the old notion of a totally interdependent community in which any change in abundance of any species is a threat to the entire community (the "rivet" hypothesis). However, wildland communities continuously receive new arrivals. The consequent readjustments don't always result in a net loss of species. Indeed, plant species richness of the California annual grasslands is probably much higher today than it was prior to the coming of European man (Johnson and Mayeaux 1992).

The introduction of exotics is not always as innocuous as the annual grasses in California's central valley (Hobbs and Huenneke 1992). For instance, the imported fire ant has certainly affected the biotic communities in many areas in the southeastern United States, where it occurs in high densities (Porter and Savignano1990, Tschinkel 1993). The imported fire ant is also a good example of how an introduced species can change genetically, thereby changing its role in the ecosystem (Mann 1994). The introduction of salt cedars (*Tamarix* spp.) into the southern Great Plains and Southwest, and their consequent monopolization of riparian zones, is definitely a case of undesirable simplification of an ecosystem (Graf 1978), possibly endangering the willow flycatcher. It is indeed difficult, if not impossible, to evaluate the consequences of a species introduction during its early stages because we generally lack detailed information on the biology of such species.

Most communities do not consist of highly coevolved species pairs, but exhibit some substitutability by species within groups (Westman 1990). This is not to deny mutualism and the existence of keystone or critical link species, but rather to acknowledge that not all species play these roles. We need to differentiate between the exotics to worry about and those that are of less worry, based on what they do. Vitousek (1990) makes a good case for concentrating on exotics that play a strong role in energy flow or nutrient cycles or that change disturbance regimes. A good example on western rangelands is cheatgrass (Billings 1990). Introduction of this winter annual grass has led to a shortening of the interannual fire cycle by about an order of magnitude. Furthermore, fires now come earlier within the year so that the chances of soil erosion are increased. The consequent lack of recovery of native perennial bunch grasses and nonsprouting shrubs such as sagebrush leads to enormous change in the biotic communities and the accompanying environments (West 1995).

CRITICAL LINK SPECIES

Critical link species are those that play a vital role in ecosystem function, regardless of their biomass, place in a food web, or possible role as a keystone species (Westman 1990). Mycorrhizal fungi are an example of a group of critical link species on rangelands. These organisms exchange carbon fixed by green plants for enhanced uptake of phosphorus. The absence of appropriate mycorrhizal species may severely inhibit the establishment and growth of the vascular plants that depend upon them. Approximately 90 percent of all vascular plants are thought to depend upon mycorrhizal mutualists. The importance of these species in rangeland ecosystems is demonstrated by the studies of Wicklow-Howard (1989), who found that repeated fires promoted by cheatgrass on land formerly covered by sagebrush steppe can lead to extinction of mycorrhizae over vast areas and impede attempts to reestablish shrubs and perennial grasses there.

It is necessary, but not sufficient, simply to identify critical link species. Quantitative knowledge of their ecological interactions and substitutability will be required if such species are to be considered in management policy. For instance, the effectiveness of the mycorrhizal-plant symbiosis can be affected by other organisms in the system. Soil collembola have been found to reduce the effectiveness of phosphorus transfer to grasses by grazing on the VA mycorrhizal hyphae (McGonigle and Fitter 1988). The same species of collembolans that graze on mycorrhizal fungi may be essential in the mineralization of nutrients immobilized in the hyphae of saprophagic fungi. Firmly establishing critical links will require addition or subtraction experiments.

The concepts of minimal and configurational structure (Pickett et al. 1989) are also worth considering. Species composition (configurational structure) within functional groups (minimal structure) may vary widely without collapse of biotic communities or ecosystems. Stennhauser (1991) has recently demonstrated how qualitatively defining stability as the maintenance of minimal structure is a practical approach to assessment of ecosystem change. Grabherr (1989) gives an example of how to proceed to identify keystone species, modules, guilds, or functional groups on rangelands, but see also the warnings of Mills et al. (1993) before undertaking this type of work.

Another possible way of quantifying ecosystem diversity is through food web complexity (Kikkawa 1986). This is because the number of feeding links reflects total productivity plus the number of links that can develop between all trophic levels in the ecosystems of interest. We have barely begun this kind of research on rangelands.

CONCLUSION

We hope to have convincingly demonstrated that diversity of services, processes, and disturbances within ecosystems is another important facet of biodiversity to consider. The importance of extinction and invasion is not equivalent for all species; it depends on what those organisms do within ecosystems. We have barely begun to understand rangelands as ecosystems. The linkage of biodiversity to ecosystem function is scarcely known in these as well as most other ecosystems (Schulze and Mooney 1993). Considerably more effort should immediately go toward identifying functional groupings, relative importances, connections, and the impacts of additions or subtractions. Loss of species is inevitable, loss of functions need not be if we understand our rangeland ecosystems well enough to prioritize our management and protection efforts. The ecosystem-level concerns are, however, but one facet of biodiversity. We acknowledge that there will be situations where preservation of species

with no obviously important role in ecosystems takes precedence (e.g., the charismatic megafauna). Such decisions will involve ethics and aesthetics more than functionality.

If sustainable development is ever to be realized, we need to find ways that natural resources can be both used and maintained. Finding balancing points would be easier if we better understood the roles that both species and other groupings play in ecosystem structure and function.

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