Understanding and Managing Rangeland Plant Communities   6

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Introduction

An understanding of plant communities and their dynamics is central to management aimed at minimizing degradation, promoting restoration or sustaining productivity of the world's rangelands. The spatial organization and temporal dynamics of communities are influenced by resource availability (e.g. water, nutrients), stresses (e.g. temperature, salinity) and disturbances (e.g. fire, grazing) as these affect plant performance. The differential responses of plants variously adapted to acquire resources and tolerate stress and disturbance affects species interactions and population dynamics (recruitment, longevity and mortality). Resource availability, stress and disturbance also vary with time and across space. Soils and topography modulate plant and community responses to these. This spatial and temporal variation produces patterns and 'behaviours' in communities and may induce fluctuation or directional change in community composition.

The challenge facing ecologists and managers is to recognize and understand the constraints imposed by these factors at various spatial and temporal scales and determine how and when they might be effectively manipulated or modified to reach desired goals. There are various approaches to achieving this recognition and understanding. This chapter will argue that: *(i) the role of nitrogen as a determinant of plant communities in rangelands has been underestimated; (ii) the importance of positive species interactions (facilitation) has been under-appreciated; and (iii) the benefits that might accrue*

from explicitly combining descriptive, experimental, monitoring and modelling approaches in a hierarchical framework have yet to be realized.

Contrasting Perspectives on Community Organization

Limiting factors: water vs. nitrogen?

Low and variable annual rainfall is a prominent feature of many rangelands. Moisture has typically been regarded as *the* limiting resource and driving force in community dynamics. However, nutrient availability may also exert a strong influence. There are clear evolutionary trade-offs between features enabling plants to tolerate nutrient-poor conditions and features conferring competitive superiority under nutrient-rich conditions (Chapin, 1980, 1993; Berendse and Elberse, 1990; Aerts and van der Peijl, 1993). Furthermore, plants can modify soil nutrient status (Hobbie, 1992) in ways which may promote or deter community change (Tilman and Wedin, 1991; Binkley and Giardina, 1998; Schlesinger and Pilmanis, 1998). Linkages between nutrient cycling and plant community dynamics may thus be strong (Rietkerk and van de Koppel, 1997; Wedin, 1999). *To what extent has our focus on water in isolation from nutrients constrained our understanding and management of plant communities?*

It is generally assumed that at lower levels of annual precipitation, above-ground net primary productivity is limited primarily by water, whereas at higher levels of precipitation, it is limited primarily by nitrogen. Hooper and Johnson (1999) tested this assumption by synthesizing results from fertilization experiments in arid, semi-arid and subhumid rangelands. Their survey found no strong evidence of a shift from a water to a nutrient limitation across a wide geographic rainfall gradient. Indeed, responses to N addition were typically positive, even at dry locations and even in years of below average rainfall. Such results suggest tight coupling between water and nitrogen and co-limitation (Chapin *et al.*, 1987; Chapin, 1991), an interpretation also supported by process-based dynamic simulation models (Schimel *et al.*, 1997).

Plant community studies that focus solely on water without accounting for plant-available soil nitrogen may be overlooking a critical factor. Contradictions in predictions of plant community response to moisture might be resolved if nitrogen is factored in. The physiological and evolutionary responses of plants to nutrient limitation and the responses of microbial decomposers to plant tissue chemistry create feedbacks that may reinforce N limitations

(Vitousek, 1982; Hobbie, 1992; Chapin, 1993). Disturbances such as grazing and fire may alter or disrupt the feedbacks between vegetation and N availability (Fig. 6.1) (Holland *et al.*, 1992; Seastedt, 1995; Wedin, 1995, 1999) and propel a community into alternate stable states (Jefferies *et al.*, 1994; Pastor and Cohen, 1997; Rietkerk and van de Koppel, 1997; Rietkerk *et al.*, 1997).

All temperate and tropical biomes receive more N via wet and dry deposition today than pre-industrially; and northern hemisphere temperate ecosystems receive more than four times that of pre-industrial levels (Holland *et al.*, 1999). Given these recent increases in N deposition, there is a pressing need to understand how water and N influence ecosystem processes both independently and interactively (Burke *et al.*, 1991; Vitousek *et al.*, 1997). If, for example, N deposition reduces or alleviates N limitations in rangelands, primary production and species composition may become more sensitive to temporal variation in rainfall and change the nature of management risk and uncertainty.
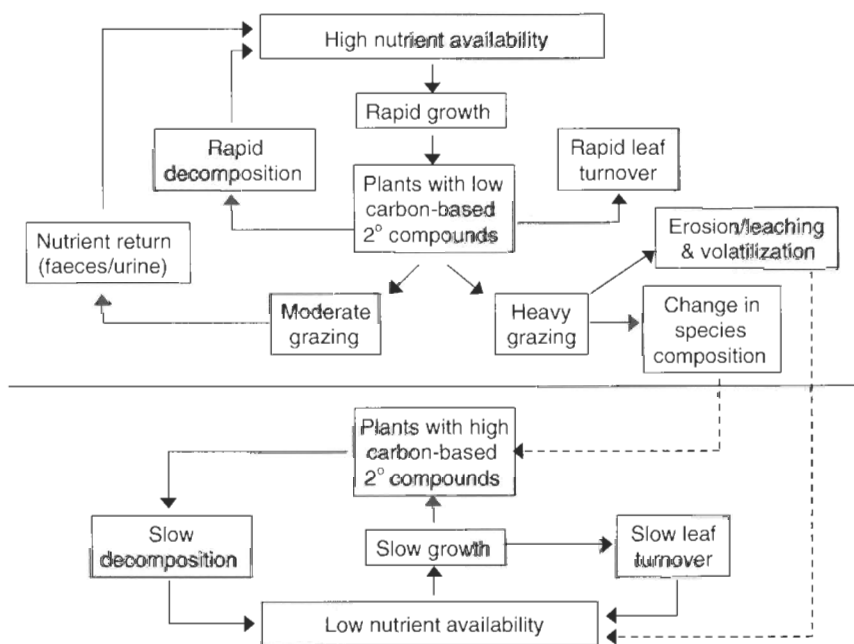

Fig. 6.1. Conceptual model of plant–soil feedback in low (upper panel) and high (lower panel) fertility sites and how prolonged heavy grazing might transform a high fertility site to a low fertility site, by altering species composition and plant–soil interactions (adapted from Chapin, 1993). In this conceptual model, nutrients, rather than water, drive community response to grazing.

Species interactions: competition vs. facilitation?

Established plants exert a sphere of influence on soils and micro-
climate in the vicinity of their canopies. This sphere of influence has
typically been viewed from the perspective of competition (Keddy,
1989; Walker *et al.*, 1989). However, plants may also serve as recruit-
ment foci and create conditions conducive to the germination,
establishment or growth of other plants. As such, *positive interactions
among species (facilitation) may play an important, but under-
appreciated role in the organization and dynamics of plant communi-
ties.* Under what conditions is facilitation likely to occur and to what
extent has the focus on competition rather than facilitation constrained
our understanding and management of plant communities?

Bertness and Callaway (1994) and Callaway (1995) persuasively
argue that evidence for the importance of facilitation in community
organization and dynamics has accrued to the point where it
warrants formal inclusion into community ecological theory. Plants
may facilitate other plants directly or actively by ameliorating
harsh environmental conditions, by altering soil properties or by
increasing availability of resources. Facilitation may be indirect or
passive if a plant eliminates competitors, introduces or attracts
other beneficial organisms (e.g. microbes, pollinators), provides
protection from herbivory, or serves as a focus for the concentration of
propagules.

Positive interactions are prominent in some communities and
conspicuously absent in others. It appears that their relative
importance varies with species traits (Callaway, 1998a) and changes
with time and the life stages of the interacting plants (e.g. Greenlee
and Callaway, 1996; Barnes and Archer, 1998) or with features such
as plant density (cf. Scholes and Archer, 1997). There may also be
variation among individuals within a community (Callaway and Tyler,
1999). Generalizations regarding facilitation, as with those regarding
competition, should therefore be made cautiously.

Interactions among plants have been shown to shift from comp-
etition to facilitation along environmental continua (Archer, 1995;
Callaway, 1998b). Facilitation may be most common in communities
developing under high physical stress and in communities with high
consumer pressure (Bertness and Callaway, 1994; Callaway and
Walker, 1997). In these situations, amelioration of stress by neighbours
may enhance growth more than competition restricts it. In intermediate
habitats, where the physical environment is relatively benign and
consumer pressure is less severe, rapid resource acquisition is
possible and competitive interactions may be a dominant structuring
force. Incorporation of facilitation into models of community organiza-
tion that are largely dominated by competition, lottery events and

fluctuations in stress and resource availability, may pave the way to clearer understanding (Fig. 6.2).

Main effects vs. interactions

Ecologists and range managers tend to view categories of variables associated with resource availability, stress and disturbance as independent 'main effects'. Consider the vast number of papers focused on the role of precipitation, the role of grazing, the role of fire, the role of
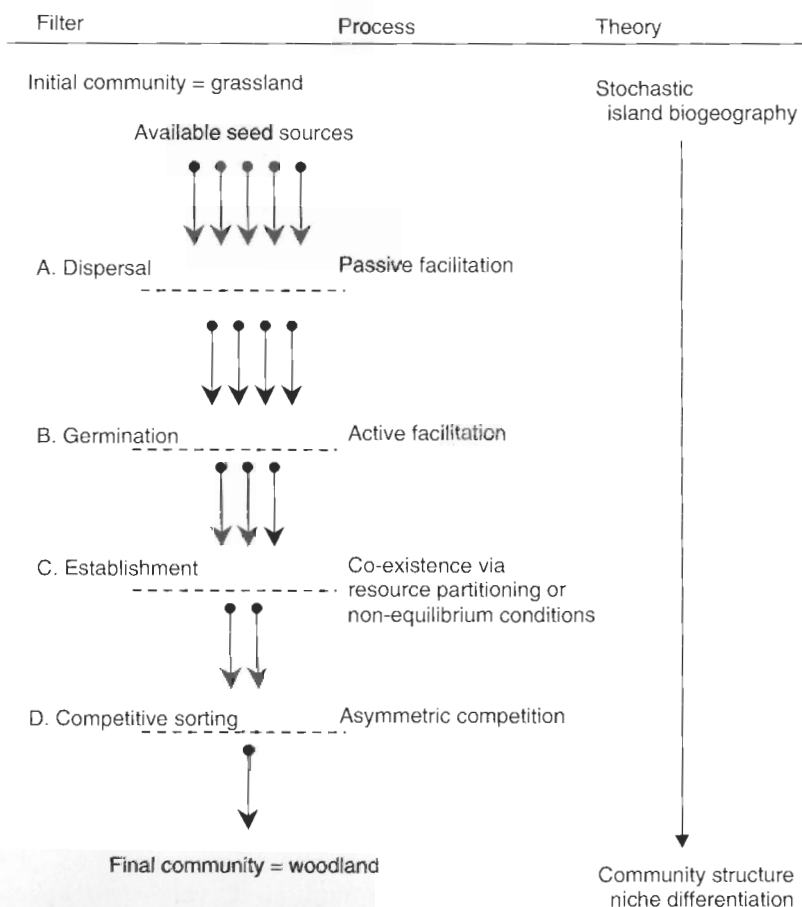

Filter	Process	Theory
Initial community = grassland		Stochastic island biogeography
Available seed sources		
A. Dispersal	Passive facilitation	
B. Germination	Active facilitation	
C. Establishment	Co-existence via resource partitioning or non-equilibrium conditions	
D. Competitive sorting	Asymmetric competition	
Final community = woodland		Community structure niche differentiation

Fig. 6.2. Conceptual model of species–environment interactions during succession from grassland to woodland demonstrating the rich array of processes and interactions that interact to affect community structure and change (based on Archer, 1995 and Stokes, 1999).

diversity, etc. in shaping plant communities. Typically, these factors are considered independently and in isolation from each other when, in fact, they are highly interactive. For example, the effects of grazing may be minimized in years of good rainfall and intensified in years of low rainfall. Grazing and rainfall will also affect fine fuel biomass and continuity and thereby fire frequency and intensity. Thus, a realistic understanding of the effects of grazing, fire or precipitation on community structure and function is contingent upon understanding their interactions.

Major funding programmes over the decades have changed the emphasis of research, yet the tendency to focus on 'main effects' persists. In the 1960s–1970s there was a focus on abiotic (climatic) factors with little emphasis on biotic effects on ecosystem structure and function (i.e. the International Biological Programme). In the 1970s–1980s, there was widespread recognition of the role of animals in affecting plant communities; however, plant–animal interaction studies were often conducted with little regard for abiotic influences (e.g. climate, nutrients and fire). To what extent has the focus on 'main effects' constrained our understanding and managing of plant communities?

Field experiments are usually restricted to examining a limited subset of possible effects, to the exclusion of dominant interactive effects. Results of field experiments are therefore highly context-dependent. O'Connor (1999) illustrates the context problem using a series of separate, long-term factorial experiments initiated in 1948, that were designed to investigate the effect of nutrients, fire, mowing and rotational livestock grazing on a grassland community. Each of the experiments clearly demonstrated that resource availability and type of disturbance had significant effects on community composition. However, despite the impressive, long-term nature of this experiment the relative importance of these independent factors remains open to debate as does the question of 'How would the community have responded if some or all of these factors had interacted?' In the absence of explicit theoretical predictions to guide experimentation, there is a preoccupation with simply demonstrating that a factor is 'important'. Preoccupation with demonstrating that specific factors are important will produce catalogues of examples. These in turn foster analyses of whether an observed phenomenon is caused by this or that factor or the relative importance of selected factors. In interacting systems, this may be fruitless enterprise as it is conceptually impossible to assign quantitative values to specific causal factors or separate them in this way (Levins and Lewontin, 1985). The emphasis should instead be on how factors interact and the nature of their interconnectedness. We should not be searching for factors *per se*. Rather, *we should be endeavouring to construct*

coherent conceptual frameworks for predicting the consequences of factor interactions.

Description vs. experimentation

Early studies of communities were primarily descriptive and quantified *how* communities looked or *how* they changed. Processes were inferred from patterns and space was substituted for time as a means for assessing community change. However, inferences from descriptive studies can be misleading (Austin, 1977; Shugart *et al.*, 1981; Likens, 1988; Cale *et al.*, 1989). Furthermore, descriptive studies often lack explanations of *why* observed community changes occur. Long-term observations can suggest importance of exogenous events (such as drought or a late freeze) on communities, without revealing how endogenous processes were modified to produce the observed response.

The following example illustrates the pitfalls of making inferences from descriptive studies. Field observations of plant distributions and soil properties in a savanna parkland landscape demonstrated that large groves of woody vegetation occurred where argillic horizons (zones of clay accumulation) were poorly expressed. Where the argillic horizon was well developed, small shrubs and grasses dominated (Archer, 1995). Soil trenches revealed that burrowing rodent and leaf cutter ant activity was substantial in soils with the poorly developed argillic horizons associated with tree groves and minimal in non-grove soils. These observations led to the 'explanation' that mixing of soils by cutter ants and burrowing rodents had disrupted a laterally continuous argillic horizon and hence promoted the development of tree groves. This explanation was logical, intuitively appealing and consistent with field data. Using the method of multiple working hypotheses (Chamberlin, 1965), it was reasoned that if this explanation were valid, the clay content of grove and non-grove soils should be comparable when summed across the entire soil profile. As it turned out, this was not the case. It therefore appears that woody plants, cutter ants and burrowing rodents were exploiting a pre-existing condition on the landscape, where for pedogenic reasons, the argillic horizon had never formed. Subsequent research has supported the latter explanation (Boutton, 1996; Stroh *et al.*, 2001).

Reductionist approaches based on experimentation and manipulation have been advocated as an alternative to descriptive approaches. The hypothesis testing approach seeks to answer the *why* question via rigorous application of the scientific method and to avoid the pitfalls exemplified in the preceding example. However, to control and manipulate the environment typically necessitates working on small

scales and over short time frames. Surveys of experimental studies reveal that about 50% have been conducted in plots 1 m² and 40% have been completed in 1 year or less (Kareiva and Anderson, 1988; Brown and Roughgarden, 1989; Tilman, 1989). Do such studies really advance our understanding of dynamic, complex communities?

Field experiments: problems and pitfalls

... there is no single, simple approach that can ever unambiguously demonstrate how or why a particular process, physical factor, or species has an effect on another element of the ecosystem ... ecological research requires a synthetic approach in which observation, experimental, and theoretical approaches are pursued in a simultaneous, coordinated, interactive manner.

(Tilman, 1989, p. 136)

We tend to measure things for which we have tools and we assume that what we measure is important. There is also a tendency to avoid rather than include stochasticity, biocomplexity and variability. Field experiments are often too short in duration, too small in spatial scale and too narrowly focused to effectively capture characteristic behaviours of communities (e.g. Watson et al., 1996]. Additional processes, undetected or not represented at the scale of the experiment, may dictate the structure and dynamics of communities at spatial and temporal scales relevant to management (Turner and Dale, 1998). *Field experiments may therefore be highly contextual, with artificialities that make their extrapolation in time and space tenuous* (Bender et al., 1984; Diamond, 1986; Yodzis, 1988; Inchausti, 1994).

For example, experiments whose results support the notion that plant species diversity enhances ecosystem productivity and resilience (Tilman and Downing, 1994; Tilman et al., 1996) have been challenged on the basis that these traits are determined largely by the most productive species in the experimental plots, irrespective of plot diversity (Aarssen, 1997; Grime, 1997). The correlation between diversity and community productivity and resilience may simply reflect the fact that the most productive species used in the study had a greater chance of being included in the more diverse plots than in the less diverse plots (Huston, 1997).

Biological variability and complex organismic interactions should be included rather than avoided in experiments, even if the price to be paid is a less clear-cut mechanistic insight. Reductionist, highly controlled experiments may contain 'hidden treatments' (Huston, 1997) and exclude or limit effects critically affecting community dynamics. Large-scale, long-term experiments focused on factor interactions, even if expensive and messy, are needed if we are to

understand plant communities at scales relevant to management and socio-economic policy. Further, there needs to be an explicit integration of experimentation with theory. In the absence of explicit theoretical predictions to guide experimentation, we end up with catalogues of important but disconnected variables. Experiments should be harnessed to adjudicate theory or major conceptual frameworks or to measure quantities that can be employed with the theory to make more specific predictions for further tests (Werner, 1998). Proliferation of small-scale, short-term experiments divorced from theory will contribute information and data to a body of knowledge, but may do little to advance our understanding.

Hierarchical perspectives

The questions before us are not whether we should do experiments in community ecology or to what extent. We should, and in abundance. Nor is the question whether experiments are the only way to contribute toward a predictive ecology. They are not.

(Werner, 1998, p. 3)

Plant communities comprise myriad interacting and interdependent elements. How do we simplify their daunting complexity to manageable proportions? Hierarchy theory is one approach (Allen and Starr, 1982; O'Neill *et al.*, 1986; Rosswall *et al.*, 1988). In this conceptual view, ecological systems are represented as a graded series with several levels of organization. An entity representing a given level of organization consists of smaller entities and is a component of a higher level of the hierarchy (Fig. 6.3).

For example, an individual plant comprises interacting leaf, stem and root subsystems. However, this same plant, if rooted in a soil along with other plants, is a component of a higher-level entity, which might be recognized as a patch. Patches arrayed across a soil type may collectively represent a community; communities are distributed along catenas to form landscapes, etc.

As this example implies, there are distinctions between structural entities at a given level of organization (e.g. between roots, stems and leaves at the plant level; between plants, animals and microbes at the patch level); and distinctions between successive levels (between leaves, plants, patches, communities). Each level of organization is characterized by processes that operate at certain spatial and temporal scales. Plant level processes would typically focus on gas exchange, water relations and allocation. Patch level processes might focus on infiltration rates, seedling establishment, competitive interactions, and herbivore forage selection. At the community level, distinctions between individual plants are lost, but runoff–runon, dry deposition,
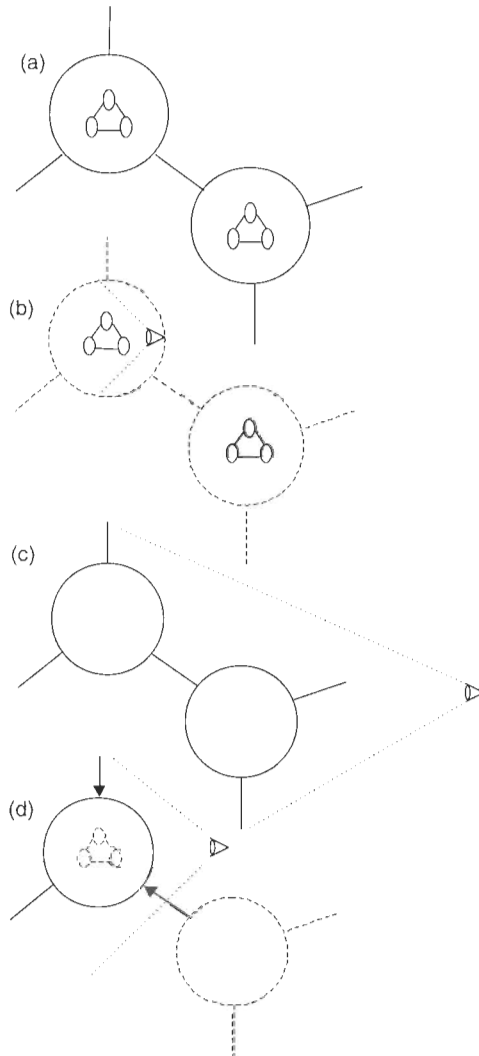
Fig. 6.3. The perspective taken on a system will influence the information accessible at various levels of organization. This hypothetical system consists of two entities, each with three parts (a). The complete system is not visible within any single observation set. Inside the surface, looking inward (b) is the only position from which the parts and their interconnections can be seen without distortion. If the observer moves far enough away from the surface, the other whole is identifiable as a separate entity, responsible for part of the environmental influence (c). Seen from outside, the parts are obscured by the intervening surface and the other entity is manifested only as an environmental influence of undefined origin (d). The eye indicates the position from which the system is observed in each case (after Allen et al., 1984, 1999).

diversity, boundary dynamics and edge effects are now recognized. Thus, higher levels in an ecological hierarchy contain, constrain, behave at lower frequencies and exhibit less bond strength than lower levels. In addition, higher levels buffer lower levels and filter environmental influences and variability (Allen *et al.*, 1984, 1999). Therefore, unexplained variance or behaviour at lower levels might be accounted for when higher order effects are explicitly acknowledged.

As with the parable of the blind men who each felt a different part of an elephant and proceeded to describe the whole without knowledge of the other parts, our perception and understanding of communities may be largely a matter of perspective. *In contrast to reductionist approaches, the hierarchical approach permits evaluation of complex systems without reducing them to a series of simple, disconnected components. No single level in an ecological hierarchy is fundamental; understanding a system at one level requires knowledge of levels both above and below the targeted level.* Interpretation of system behaviour at one level of organization without consideration of adjacent levels is therefore out of context. For example, the views of Clements, Gleason and Tansley may be more complementary than contradictory when viewed from a hierarchical perspectives (Fig. 6.4) (Hoekstra *et al.*, 1991).
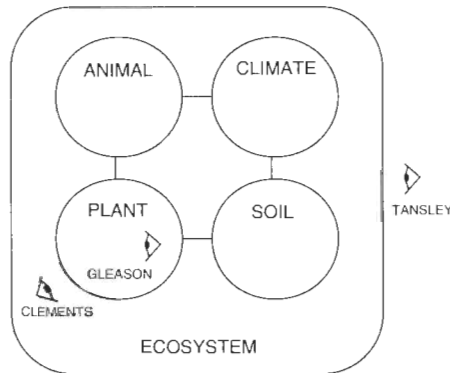

Fig. 6.4. A schematic representation of the different scales of perception involved in the individualistic concept of community (Gleason, 1926), viewed from inside the community, where the focus is on the autonomy of the component species; the superorganismal concept of community (Clements, 1905), viewed from outside the community so as to emphasize its integrity; and Tansley's (1935) conception of the ecosystem, viewing the system from a greater distance, so that the autonomy of the biota is obscured as it is integrated with the physical environment. The three images of an eye represent the locations of the observers (from Hoekstra *et al.*, 1991).

Holistic and reductionist approaches should not be viewed as mutually exclusive. Each provides a unique perspective. The reductionist approach dissects lower levels of organization and provides mechanistic explanations and insights into how systems work. However, reductionist studies strictly looking 'inside' the system do not see the whole and its emergent properties. The holistic approach views a system in the context of the higher levels in which it is embedded, and provides insight into the significance of phenomena at lower levels. The search for mechanisms should therefore be balanced by concern for significance (Passioura, 1979; Lidicker, 1988). Studies focused at one level of organization without regard for higher levels can thus generate vast amounts of information, but little understanding.

The Way Forward

We have a wealth of detailed observations on the natural history of our planet, but are only beginning to uncover (or invent) the general principles which can organize this mass of observations.

(Keddy, 1989)

We are drowning in information, while starving for knowledge. The world henceforth will be run by synthesisers, people able to put together the right information at the right time, think critically about it, and make important choices wisely.

(Wilson, 1998)

The above quotes indicate that what is needed is more understanding and new perspectives, not simply more data. Community composition and dynamics are outcomes of the interactions among constellations of driving variables. Therefore, extrapolations from context-dependent experiments and descriptive studies should be made with caution, and static management 'prescriptions' based on case studies should be viewed with scepticism. How do we then progress with understanding and managing plant communities?

The preoccupation with 'main effects' is partially due to logistical constraints: the duration of contract/grant funding typically relegates most studies to short (2–3 year) time frames and a very specific, narrow focus. A clear articulation of the need for more comprehensive studies designed to focus on key interactions may be a necessary first step in overcoming this logistical barrier. *Descriptive, experimental and modelling approaches have advantages and disadvantages, each providing perspectives the others cannot. Natural resource administrators and science programme managers should therefore promote multidisciplinary ventures that proactively integrate these approaches* (Fig. 6.5).
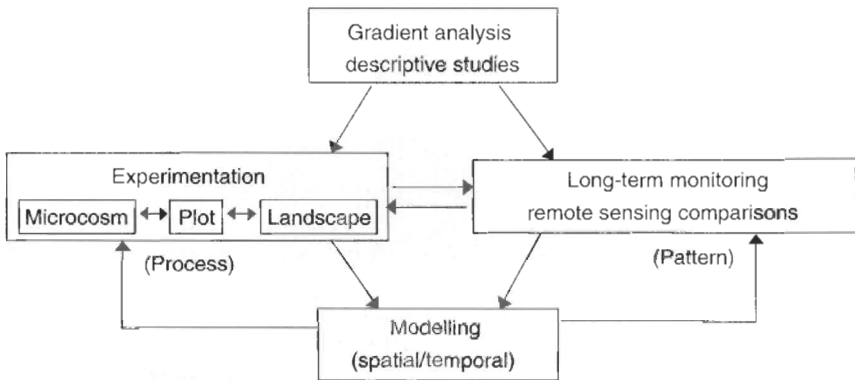
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                    ┌──────────────────────┐
                    │  Gradient analysis   │
                    │ descriptive studies  │
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Fig. 6.5. Conceptual integration of descriptive, experimental and modelling approaches. To date, most of these approaches have been used in isolation. Gradient analysis may suggest hypotheses, which could be tested via experimentation and monitoring. These, in turn, may suggest new suites of environmental variables for gradient analysis while providing input for simulation models. Simulation models and modelling experiments feed back to help prioritize and refine experiments and monitoring protocol. Linked remote sensing–modelling approaches hold the promise to provide monitoring of function as well as structure over large areas (e.g. Asner *et al.*, 1998; Wessman, 1992; Wessman *et al.*, 1997). Experimentation and monitoring should be conducted at spatial and temporal scales appropriate to specified levels of hierarchical organization (Fig. 6.3). Experiments should be harnessed to adjudicate theory or major conceptual frameworks or to measure quantities that can be employed with the theory to make more specific predictions for further tests.

The 'multiple working hypotheses' approach (Chamberlin, 1965; Ward, 1993) has clear utility in community ecology, yet remains under-utilized. Astronomers, geologists, climatologists and ocean-ographers have achieved marked successes in inferring process from pattern, in constructing and evaluating complex models, and in testing hypotheses without the benefit of experimental manipulation and replication (Brown, 1994). We must move beyond our traditional, simplistic 'either–or' mentality (either water or nitrogen as *the* limiting factor; either competition or facilitation as *the* driver of species inter-actions; either descriptor or experimentation or modelling as *the* approach to studying communities). Perspectives which embrace the duality of resource constraints (e.g. water *and* nitrogen) and processes (e.g. competition *and* facilitation) as determinants of plant communi-ties and which integrate complementary approaches for studying these (e.g. experimentation *and* description *and* modelling as guided by theory) are likely to provide us with a richer, more robust understanding of plant communities and ecosystems.

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