18

Future Directions in Jornada Research: Applying an Interactive Landscape Model to Solve Problems

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The long history of research at the Jornada Basin (through the Agricultural Research Service [ARS] since 1912, New Mexico State University in the late 1920s, and joined by the Long-Term Ecological Research [LTER] program in 1981) has provided a wealth of information on the dynamics of arid and semiarid ecosystems. However, gaps in our knowledge still remain. One of the most perplexing issues is the variation in ecosystem dynamics across landscapes. In this concluding chapter to this volume, we propose a new conceptual model of arid and semiarid landscapes that focuses explicitly on the processes and properties that generate spatial variation in ecosystem dynamics. We also describe how our framework leads to future research directions.

Many studies have documented variable rates and patterns of shrub invasion at the Jornada as well as at other semiarid and arid regions of the world, including the Western United States, northern Mexico, southern Africa, South America, New Zealand, Australia, and China (York and Dick-Peddie 1969; Grover and Musick 1990; McPherson 1997; Scholes and Archer 1997; see also chapter 10). In some cases, shrub invasion occurred very rapidly: At the Jornada, areas dominated by perennial grasses decreased from 25% to < 7% from 1915 to 1998 with most of this conversion occurring prior to

1950 (Gibbens et al. 2005; Yao et al. 2002a). In other cases, shrub invasion occurred

slowly, and sites were very resistant to invasion; for example, perennial grasses still

dominate on 12 out of 57 research quadrats originally established in black grama

(*Bouteloua eropoda*)grasslands in the early twentieth century (Yao et al. 2002b). Soil

texture, grazing history, and precipitation patterns are insufficient to account for this

variation in grass persistence through time (Yao et al. 2002a). It is equally perplexing

why many attempts to remediate these shrublands back to perennial grasses have led to

failure, whereas some methods worked well, albeit with long (> 50 year) time lags

(Rango et al. 2002; see also chapter 14).

Although variations in vegetation dynamics and shrub invasion are the most well

known, other lesser known aspects of arid and semiarid systems have been found to be

quite variable as well. In arid systems, aboveground net primary production (ANPP) can

vary three- to fivefold, both between years at the same location and within the same year

at different locations (Huenneke et al. 2001, 2002; see also chapter 11). Given the

importance of arid and semiarid systems to current global issues, including carbon

dynamics (Houghton et al. 1999; Pacala et al. 2001; Jackson et al. 2002), loss of

biodiversity (Whitford et al. 2001), invasion of exotic species (DiTomaso 2000; Masters

and Sheley 2001), wind and water erosion of soil and nutrients (Schlesinger et al. 1999;

Wainwright et al. 2000), and emission of dust loads to the atmosphere (Gillette et al.

1992; Tegen et al. 1996; Gillette and Chen 2001), there is a critical need for a better

understanding of ecosystem patterns and dynamics at multiple spatial and temporal

scales. This improved understanding is critical to our ability to manage these landscapes

as well as to make predictions about future dynamics with local, regional, and global impacts.

In this chapter, we describe and illustrate the utility of a conceptual framework that focuses on three interrelated aspects of landscapes: (1) feedbacks among plants, animals, and soils generated from interactions among biotic processes, a heterogeneous physical template, and the disturbance regime across a range of spatial and temporal scales; (2) neighborhood or contagious processes that generate fluxes and flows within and among spatial units; and (3) landscape characteristics, including the structure and spatial distribution of spatial units as well as the landscape context or the condition of the study area of interest relative to its surroundings that modify the transfers of materials.

A key feature of our conceptual model is that it facilitates an evaluation of the relative importance of each of these three aspects and recognizes that some or all may not be sufficiently important to be included for any given problem. Although arid and semiarid landscapes consist of a complex mosaic of vegetation, soil, and animal interactions, the errors in prediction that results from including poorly understood, noncritical spatial information do not warrant a complex model for all parts of a landscape. We first describe our spatially interactive model and compare it to previous models, and then we show how to identify the landscape locations where spatial processes and information (i.e., vegetation–animal–soil feedbacks, neighborhood processes, and landscape characteristics) are needed to understand and predict ecosystem dynamics. The local, regional, and global applications of our interactive landscape model to old and new problems are also discussed.

Current Models of Arid and Semiarid Systems

Complex interactions among a number of factors (effects of large and small animals, drought, fire, climate change, and soil properties) are often invoked to explain and predict heterogeneity in arid and semiarid landscapes. The issue of shrub invasion has been addressed by a number of authors (Humphrey 1958; Schlesinger et al. 1990; Allred 1996; Van Auken 2000; see also chapter 10), yet a general consensus does not exist regarding the key factors controlling different outcomes of shrub invasion under similar conditions. It is readily acknowledged that the problem is complicated by the presence of positive feedbacks and nonlinear thresholds (Archer 1989, 1994; Archer et al. 1995; Schlesinger et al. 1990; Reynolds et al. 1997; Rietkirk and van de Koppel 1997).

Inherently high spatial and temporal variation in the physical template (climate, soils) and disturbance regime (e.g., fire) plays an important role in ecosystem dynamics. Periodic droughts on 20–60-year cycles have variable effects that depend on the severity and length of the dry period as well as on confounding factors, such as livestock grazing (Herbel et al. 1972; Woodhouse and Overpeck 1998; Reynolds et al. 1999[a]; Gibbens et al. 2005). Precipitation also has high variability between years; for example, as little as 26 cm of rain fell in one year (1990) followed by 41 cm at the same location the next year (1991) in the Jornada Basin. Annual maximum daily rainfall at the Jornada also has high variability that is not related to mean average rainfall of the basin (chapter 3). Short-duration, spatially variable convective storms can also result in marked vegetation response across a landscape within a year. This fine-scale spatial variation in

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[a] Reynolds et al. 1999a or 1999b? See Refs for book.

precipitation often translates into long-term patterns in ecosystem dynamics, such as highly variable spatial patterns in ANPP (Ludwig 1987; Huenneke et al. 2001, 2002).

Soil properties are also spatially and temporally heterogeneous. Arid landscapes are complex mosaics of soils of highly variable age formed from diverse parent materials and further modified by extensive redistribution by both wind and water (Gile et al. 1981; McAuliffe 1994; Wondzell and Ludwig 1995). Steep slopes exacerbate the effect of high-intensity convective storms (Wondzell et al. 1996). Even subtle differences in elevation (< 0.6° slope) combined with plant–soil water feedbacks can generate "striped" patterns in vegetation (Montaña et al. 1990; Aguiar and Sala 1999). The disturbance regime is also highly variable; spatial variation in fires produces nonuniform effects on the vegetation. Lightning-ignited fires occur primarily in grasslands where fuel loads are sufficiently high and spatially continuous to carry a fire. Historically, fire may have played an important role in limiting shrub invasion, but the current dominance by shrubs throughout many arid landscapes limits the ability of fires to spread (Drewa et al. 2001).

The well-known resource-redistribution model of Schlesinger et al. (1990) incorporates both spatial variation in the physical environment and disturbance regime as well as positive plant–soil feedbacks in explaining desertification dynamics. This model focuses on small patches dominated either by a grass plant, a shrub, or bare area. As grasslands degrade, often associated with invasion by shrubs, patches of bare soil appear. Wind and water remove soil nutrients from these bare areas, and nutrients accumulate under individual shrubs to generate local islands of fertility. Grazing and drought act to move the system toward desertified shrublands, whereas the exclusion of grazers and

extended wet periods favor grasslands. A basic assumption of this model is that all

patches of one type (i.e., grass, shrub, and bare) function similarly. The scale of the most

important heterogeneity is the contrast between plants and bare interspaces; smaller and

larger spatial scales are assumed to be relatively homogenous. Thus, heterogeneity within

an individual plant is ignored, and landscape-scale patterns that result from plant-scale

interactions are usually determined through linear extrapolation. No additional processes

are assumed to be needed to extrapolate beyond the scale of an individual plant or area of

bare soil. This model has been successfully applied to a number of ecosystem types and

to a range of ecological problems in a variety of arid and semiarid systems at two spatial

scales: the plant-interspace scale, where individual grasses and shrubs are compared, and

the landscape scale, where large areas of relatively homogeneous grasslands and

shrublands are compared (e.g., Augustine and Frank 2001; Hirobe et al. 2001; Maestre et

al. 2001, 2002; MacGregor and O'Connor 2002; Maestre and Cortina 2002; Neave and

Abrahams 2002).

Other models of arid landscapes include spatial and temporal heterogeneity in

physical factors and disturbances at multiple scales, as well as redistribution of materials

within and among spatial units. These landscape models typically aggregate plants into

patches based on different characteristics (e.g., size, density, configuration, interpatch

distance). Transfers of materials between patches can affect landscape function and

response to disturbance (Ludwig et al. 1997; Reynolds et al. 1997; Reynolds and Wu

1999).

Interactive Model of Arid and Semiarid Landscapes

Although previous models have been successful in explaining certain aspects of arid and semiarid ecosystems, they are insufficient to account for the variation and complexity observed in dynamics across a range of spatial and temporal scales. We propose that a new model of arid and semiarid ecosystems is needed to understand these complex dynamics, predict future dynamics, and make effective management decisions. The new model builds on previous models, in particular the model of Schlesinger et al. (1990), but explicitly includes (1) variation in biotic and abiotic processes and the disturbance regime as well as feedbacks among these system components, (2) landscape characteristics, and (3) contagious or neighborhood processes that connect different plants, patches, and landscape units (figure 18-1). Our focus is on understanding and predicting variations in ecosystem properties and dynamics and not just predicting average conditions through time or across a landscape.

In our conceptual model, landscapes are structured hierarchically and consist of increasingly larger spatial units, from individual plants to patches or patch mosaics to landscape units or small watersheds (figure 18-1). The smallest scale is a plant or its associated interspace, the scale at which much of the research has been conducted at the Jornada. The next scale of interest is the assemblage of similar plants and interspaces into patches. At the Jornada most patches are dominated by one of several species of shrubs (mesquite *Prosopis glandulosa*, creosotebush *Larrea tridentata*, and tarbush *Flourensia cernua*) or grasses (black grama and tobosa *Pleuraphis mutica*). These patches vary in size from several individual plants (< 5 m^2) to several hundred individuals ($> 1,000$ m^2).
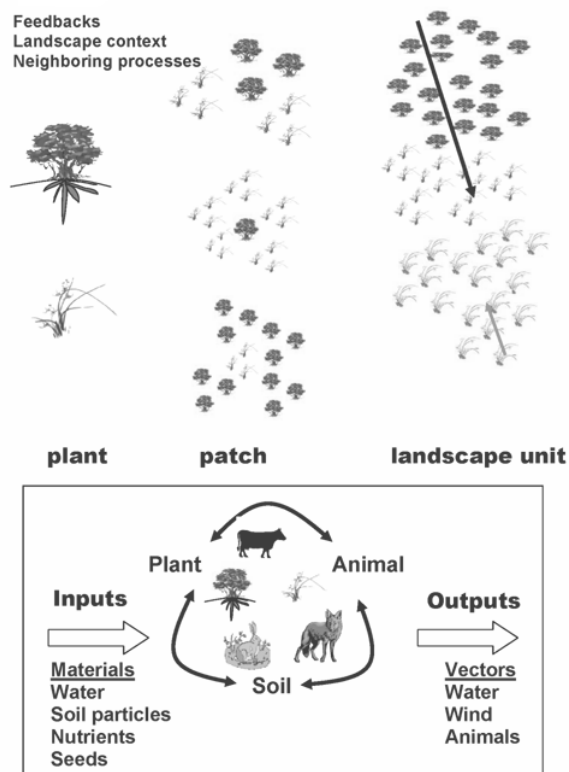
Fig. 18-1. Interactive landscape model includes the importance of plant-animal-soil feedbacks, landscape context, and contagious or neighbor processes for a hierarchically structured landscape that consists of individual plants, patches, and landscape units. Positive and negative feedbacks result from complex interactions among plants, animals, and soil properties and processes across a range of spatial scales. Water, soil particles, nutrients, and seeds are redistributed among spatial units by water, wind, and animals. Landscape context is represented in the figure by the adjacency of different patch types (grasses, shrubs) where the patch response depends on the characteristics of neighboring patches. In the case of landscape units, soil particles can move easily by wind action through open canopy shrub patches (black line) with the resulting deposition of soil in adjacent grass patches. Movement of soil between different types of grass patches is very limited. Wind becomes relatively unimportant if the direction of the prevailing winds is from the opposite direction (red line), due to little movement of soil between patches.

The next scale (landscape unit) consists of a number of interacting patches.

Spatial variation within a landscape unit, such as small depressions, can collect water and

nutrients, resulting in patchiness in soils and vegetation (Wainwright et al. 2002). The

configuration of patches (i.e., size, number, and adjacency or between-plant distance) can

have important effects on patch dynamics as well as on the function of the landscape unit.

Important landscape units at the Jornada are bajadas, sandy basins, and playas. Landscape

units are generally equivalent to ecological sites (USDA NRCS 1997) and are typically

the unit of most interest for management. Thus, a landscape such as the Jornada Basin

consists of a mosaic of interacting landscape units, each containing a mosaic of

interacting patches that consist of a mosaic of interacting individual plants and bare areas.

The dynamics of each spatial unit are determined by local physical and biotic

factors within the unit and transfers of materials among units (figures 18-2 and 18-3).

Local physical factors that exert major controls on semiarid and arid ecosystem dynamics

include geomorphology and soils, precipitation, temperature, and disturbance history.

Geomorphic constraints include parent material, elevation, and slope aspect, length, and

steepness that control the location of runoff and run-in areas (Monger 1999; see also

chapters 4 and 7). Soil characteristics determine (1) the capture, retention, and supply of

water; (2) the supply of nutrients through mineral weathering and organic matter

mineralization; (3) erosion rates; and (4) the environment for root growth and soil biotic

activity. Local precipitation inputs and temperature can vary among landscape units due

to differences in elevation and location relative to areas with high topographic relief.
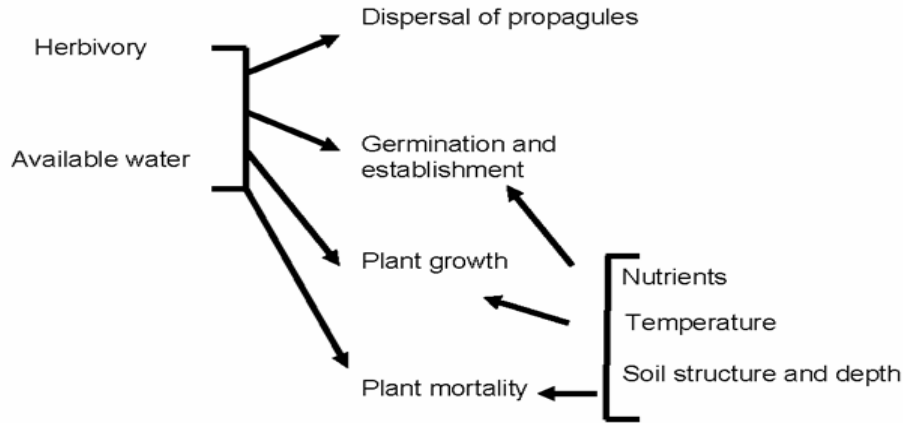
Fig. 18-2. Conceptual model of within-spatial-unit controls on ecosystem structure and dynamics.
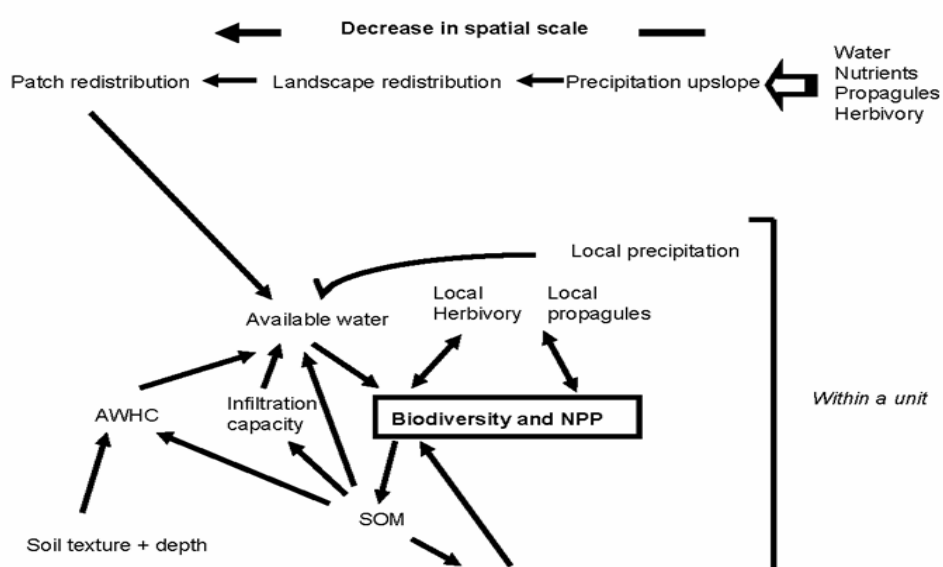

Fig. 18-3. Conceptual model of flows of materials within and among spatial units. Water, nutrients, propagules, and herbivory are spatially distributed across a landscape, and contribute to localized inputs within each landscape unit. Redistribution of water is shown as an example. Within a spatial unit, these materials exert controls on biological processes that influence patterns and dynamics in ecosystem properties, such as biodiversity and aboveground net primary productivity (NPP).

Disturbance history is particularly important in areas such as the Jornada, where active

management has occurred for decades.

Biotic Processes, Interactions, and Feedbacks

Interactions and feedbacks among physical factors and biotic processes are critical to

dynamics both within and among spatial units (figures 18-2 and 18-3). Here we focus on

plant, animal, and soil processes that generate positive and negative feedbacks.

Plant–soil feedbacks are commonly associated with shrub invasion. As shrubs

invade an area, resources become concentrated beneath shrubs and are less available to

grasses, thus resulting in a positive feedback to shrub persistence (Schlesinger et al.

1990). Feedbacks between herbaceous species and soil properties can also result in

positive feedbacks to grasses (Montaña 1992). For example, an increase in summer

precipitation may promote the establishment of short-lived herbaceous species on some

shrub-dominated sites (Peters and Herrick 1999b). This increase in plant biomass will

result in an increase in soil organic matter and infiltration capacity of the soil with

feedbacks to plant-available water and perennial grass establishment and recovery

following shrub invasion. Plant–soil water feedbacks are also important in generating

striped or spotted patterns in vegetation (Montaña 1992; Aguiar and Sala 1999).

Feedbacks among animals, plants, and soils are also important across a range of

spatial scales (van de Koppel et al. 2002). Large herbivores respond to individual plants,

patches, and landscape units that are often nonuniformly distributed across the landscape

(Senft et al. 1987; Bailey et al. 1996). The response of large animals depends on the

distribution of these spatial units of forage quality and quantity as well as abiotic features,

such as topography and distance to water. Large animals can have major impacts on the vegetation and soils at multiple spatial scales. For example, the expansion of native shrubs into perennial grasslands occurs as a result of cattle (*Bos*) consuming seeds from species such as honey mesquite that have palatable pods. Viable seeds that pass through the animal's digestive tract can be redistributed at large distances from the source plant population. The dispersal of mesquite seeds followed by establishment and growth of adult plants in combination with herbivory that reduces the cover and competitive ability of grasses would lead to reduced forage availability with a negative feedback to cattle production and use of that area (Walker et al. 1981; Brown and Archer 1999).

Nonlinear interactions and feedbacks between small animals and the vegetation often result in complex ecosystem dynamics (Brown and Morgan Ernest 2002). For example, a high density of bannertail kangaroo rats (*Dipodomys spectabilis)* in grasslands versus a greater abundance of jackrabbits *(Lepus)* and rodents following shrub invasion (Moroka et al. 1982; Whitford 1997) has important effects on patterns and intensity of herbivory, granivory, and seed dispersal (chapter 12). Soil disturbances by small animals can alter soil wind and water erodibility through digging and tracking across the surface (Belnap and Gillette 1998; Neave and Abrahams 2001). These modifications in soil water availability can influence plant growth with feedbacks to animals.

Neighborhood Processes

Neighborhood processes affect the redistribution of materials across a landscape. Transfers of material can occur within as well as among spatial units (patch to patch) and between hierarchical levels (plant to patch and vice versa) (figure 18-3). Selective

grazing on individual plants followed by fecal deposition at the patch scale can disperse

materials from small to large areas and connect distant areas. By contrast, indiscriminate

grazing at the patch scale followed by fecal deposition and localized seed germination

within a bare area is a form of disaggregation from large to small areas. These transfers

are particularly important in arid landscapes with high topographic and soil variation

combined with intense, short-duration water and wind events that lead to redistribution of

soil and water across a landscape (chapters 7 and 9). Furthermore, large and small

animals are very effective at redistributing seeds and nutrients across spatial scales

(chapter 12).

The major vectors of redistribution are water, wind, small and large animals, and

disturbances such as fire and human activities (figure 18-3). Soil particles, water,

nutrients, plant litter, and seeds are heterogeneously distributed across a landscape and

contribute to localized inputs within each spatial unit. We discuss each of the vectors that

generate neighborhood processes first, followed by the importance of landscape

characteristics in modifying these rates of transfer.

Water

The horizontal transport of storm-water runoff across arid landscapes and its ultimate

deposition—either as a contribution to soil water or to immediate evaporation to the

atmosphere—is crucial to determining the availability of water for plant growth and

reproduction. Water is also an important transport mechanism for nutrients, soil particles,

and seeds. Increased nitrogen losses from desert hill slopes have been documented as

grass cover declines and shrubs invade (Schlesinger et al. 1999, 2000). Erosion and

deposition of soil particles occur across multiple spatial and temporal scales, from the

redistribution of water between plants and bare interspaces to the movement of water in

channels or rills within patches and in arroyos that connect landscape units (Schlesinger

and Jones 1984; Wainwright et al. 2002; Parsons et al. 2003; see also chapter 7). Water is

also an important dispersal agent for seeds, in particular for large-seeded species, such as

creosotebush and sideoats grama (*Bouteloua curtipendula*) (Gutierrez-Luna 2000).

Wind

Redistribution of soil particles by wind has been well documented at the Jornada, in

particular for sandy soils in mesquite shrublands (Marticorena et al. 1997; Okin and

Gillette 2001). Other soils are also susceptible to wind erosion but are usually protected

by vegetation or a strong physical or biological crust. Disturbance by cattle and humans

is very important to note because it removes the protective vegetation and disturbs the

soil surface, exposing and creating more wind-erodible particles. Wind can also

redistribute nutrients, both locally between plants and interspaces and regionally or

globally through atmospheric circulation patterns (Gillette et al. 1992; Okin and Gillette

2001; see also chapter 9). Furthermore, seeds of many herbaceous species have

adaptations for wind dispersal (Howe and Smallwood 1982).

Small and Large Animals

Animals are effective agents of seed dispersal and redistribution of soil resources across

spatial units. Cattle consume seeds of both shrubs and grasses and can deposit viable

seeds in feces at large distances (several km) from the seed source (Janzen 1982;

Chambers and MacMahon 1994). Small animals (rodents and lagomorphs in particular)

can also have major impacts on ecosystem dynamics across multiple scales (Brown and

Morgan Ernest 2002; Yates et al. 2002). Furthermore, small animals have spatial and

temporal distributions that may or may not mirror large animal distribution patterns

(chapter 12). Thus, complex interactions can occur within and across spatial scales.

Disturbance

Fire is a multiscale phenomenon that responds to vegetation fuel load and to

environmental conditions of wind speed, temperature, and humidity that also vary

spatially and temporally. In addition to direct effects on vegetation, fire influences

transfers of materials by modifying animal behavior that affects spatial patterns in

nutrient cycling dynamics (McNaughton 1985). By reducing plant cover, fire increases

the redistribution of soil particles through wind and water erosion (Johansen et al. 2001;

Whicker et al. 2002). Fire also releases particles into the atmosphere that can affect

regional air quality (Wotawa and Trainer 2000).

Human activities also generate disturbance with potentially large impacts on

transfers of materials. Traditionally managed as rangelands, aridlands are subject to

increasing pressure for development and recreational use (Maestas et al. 2001). These

human activities alter vegetative cover and biodiversity with increasing fragmentation of

the landscape, resulting in increased wind and water erosion, as well as modifications to

natural transport processes and movement of plants and animals. Dust loads in the

atmosphere also increase during dry, windy periods with increasing urbanization and

clearing of marginal land for industry and agriculture; this sequence of events occurred

following the 1930s drought and has been cited as the primary cause of increases in suspended particulate matter in urban areas in the Southwestern United States.

Landscape Characteristics

The relative importance of transfers of materials within and among spatial scales is affected by (1) landscape characteristics, including structure (size, shape, and type of spatial units); (2) spatial distribution or configuration of spatial units; and (3) the context or location and characteristics of a study area relative to its surroundings or nearby areas. These characteristics influence the connectivity of the landscape by modifying the ability of vectors of redistribution (water, wind, animals, and disturbance) to move materials horizontally. Highly connected landscapes consist of a mosaic of spatial units distributed in such a way as to promote the movement of materials via spatial processes, whereas landscapes with low connectivity may have barriers or spatial configurations of units that restrict horizontal movement of materials. Highly connected landscapes for one vector, such as water, may have low connectivity for another vector, such as animals.

Landscapes with high connectivity can amplify an environmental driver to result in spatially nonlinear responses and a cascading effect where the rate of movement across the landscape is faster than expected based on a linear extrapolation from small-scale responses. By contrast, disconnected landscapes can buffer environmental drivers to result in a slower rate of movement than expected. For example, a fire that occurs during periods of low humidity, strong winds, and high temperatures can spread quickly across a landscape with highly connected fuel load. A landscape with a patchily distributed fuel load will limit the rate and spatial extent of the fire.

The relative importance of different contagious processes in generating these

spatial nonlinearities and cascading effects can change through time. For example, at the

Jornada, a 250-ha cattle exclosure was constructed in 1933 such that the northwest part of

the exclosure was dominated by grassland and the southern part was dominated by honey

mesquite (figure 18-4). Although cattle were excluded from the exclosure, mesquite

continued to recruit and expand in the surrounding pasture that was grazed as well as in

the exclosure as a result of the dispersal of mesquite seeds from small animals. Local

dispersal from mesquite plants within the exclosure at the time of construction was also

likely. From 1948 to 1987 the grazed pasture continued to fill in with new mesquite

plants, and the established plants grew larger. At some point between 1987 and 1998, the

density and spatial configuration of mesquite plants crossed a critical threshold such that

wind erosion became prevalent and coppice dunes developed throughout both the grazed

pasture and the nearby exclosure. These legacies, such as the historic location of shrub

communities, can be particularly important in understanding current patterns in

vegetation and soils.

Landscape context can directly affect ecosystem dynamics: A barrier may restrict

animal movements from one vegetation type to another. A grass patch adjacent to a sandy

mesquite patch is more likely to suffer negative impacts of sand deposition than a similar

grass patch adjacent to a stable creosotebush-dominated area. Indirect effects of

landscape context are also important. Few studies have included landscape context when

examining factors influencing shrub invasion and grass persistence. Most studies have

examined plot-level characteristics and have not accounted for the influence of the
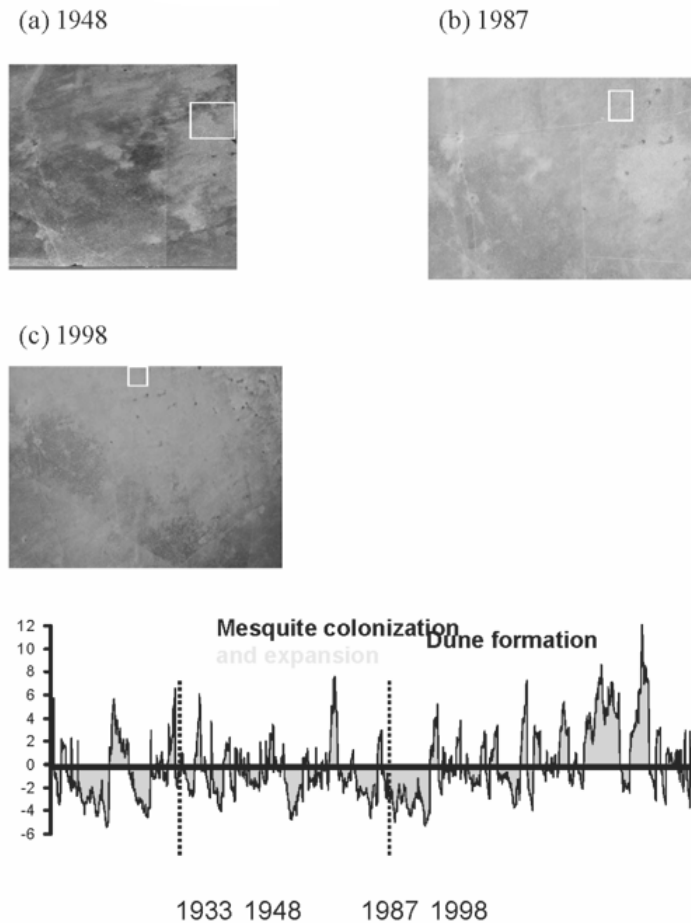
Fig. 18-4. Images from natural revegetation exclosure through time showing nonlinear dynamics and importance of different spatial processes. A 1-mile by 1-mile exclosure was constructed in 1933 on the Jornada where the northwest part of the exclosure was dominated by grassland and the southern part was dominated by honey mesquite *(Prosopis glandulosa)*. Although cattle were excluded from the exclosure depicted by the white rectangle, mesquite continued to recruit and expand into the surrounding pasture that was grazed, primarily from east (right) to west (left). Almost 40 years were required for a large area to be dominated by mesquite dunelands shown in 1987 in the right side of the image. These dunelands then crossed a threshold and rapidly expanded; within 11 years the dunelands had dominated much of the pasture. Placement of the exclosure in the western part of the pasture would have delayed the expansion of dunelands into the exclosure but not as a result of protection from grazing.

surrounding area. However, the very slow recovery (> 50 years) of black grama

following shrub removal (Gibbens et al. 1993; Havstad et al. 1999) is likely related to the

small amount of black grama initially within the plots and the lack of a significant seed

source of this species within dispersal distance of the plots (Havstad et al. 2003). A recent

analysis showed that distance to shrubland in 1915 was the best predictor of grass

persistence in 1999; the farther a plot was from an existing shrubland, the greater the

probability that grasses would persist through time (Yao et al. 2002a). Other explanatory

factors commonly used in shrub invasion studies, such as soil texture, grazing intensity,

and precipitation, were less important than distance to the nearest shrub-dominated areas.

The importance of landscape context is also illustrated in figure 18-4: Placement of the

exclosure in the western part of the grazed pasture would have delayed the expansion of

dunelands in the exclosure but merely as a result of distance from the advancing dunes

and not protection from grazing.

Simplifying Complex Landscapes: How Do We Deal with Variation?

A particularly important part of our model is that spatial information is not needed for all

parts of a landscape. Although arid and semiarid landscapes are complex mosaics of

plants, soil, and animal interactions across spatial scales, it is not necessary and can even

be detrimental to include spatial information for all locations on a landscape. The

collection of spatial information on multiple ecosystem components (plants, animals,

soils) across a range of spatial and temporal scales, including transfers of material among

spatial units, is a time-consuming and costly venture. Furthermore, the inclusion of

parameters, especially those that are poorly understood, will increase the errors

associated with managing a large number of parameters and their estimation (O'Neill

1979; Gardner et al. 1980; Reynolds and Acock 1985). Finding the balance between

errors of omitting key information and errors of including poorly known or measured

parameters remains a critical challenge in ecology.

Our approach to simplifying complex landscapes is to determine the locations on

a landscape where all three aspects of spatial information must be known for predictions

to be accurate. We identify the key processes and their feedbacks that must be measured

for each location. Management decisions and intensive sampling can then focus on those

locations and key processes. Predictions for the remainder of the landscape can be

obtained using estimates from representative sites that are extrapolated to similar areas

using nonspatial and spatially implicit methods. Nonspatial methods using linear

extrapolations are useful for locations where landscape characteristics and neighborhood

processes, including feedbacks, are relatively unimportant (Lieth and Whittaker 1975;

Schlesinger et al. 1990). Spatially implicit methods are needed when information on

landscape characteristics is important, such as distance to the nearest shrubland, but not

neighborhood processes and feedbacks. Spatially explicit methods are necessary when

landscape characteristics, neighborhood processes, and feedbacks are important.

One approach to identifying critical locations and determining important spatial

processes is to combine remotely sensed images with field data and spatial databases

residing in a geographic information system. For example, remotely sensed images

combined with field estimates of ANPP can be used both to determine the most

appropriate vegetation index for each of the major ecosystem types and to identify the

locations (hot spots) with extremely low and high ANPP values for each ecosystem type.

Spatial databases can be used to determine the key processes operating to generate these

extremely low or high values. Correlating indices from the remotely sensed images with

the spatial databases can confirm the greater importance of spatial processes at these key

locations compared with the rest of the landscape. This method has been used

successfully to determine that different processes are important for different ecosystem

types and for different time periods (wet versus dry years) (Peters et al. in preparation).

Identifying these locations and key processes is the first step in simplifying complex

landscapes to prioritize management decisions and guide research questions and

experimental designs.

Future Directions: Applications of Interactive Landscape Model to Old and New Problems

Our conceptual model of interactive landscapes provides new insight into several

perplexing problems in arid and semiarid systems and promises to guide future research.

Here we describe the use of this approach in addressing three pressing ecological issues:

shrub invasion, remediation, and carbon storage and dynamics.

Shrub Invasion

Historically, landscapes of the Southwestern United States were a mosaic of grasslands

and shrublands with a much greater proportional area dominated by grasses than occurs

at present (Hastings and Turner 1965; Grover and Musick 1990; Gibbens et al. 2005).

This mosaic was due to interactions among vegetation characteristics with topography

and landform that influenced water availability (Gardner 1951; York and Dick-Peddie 1969; Stein and Ludwig 1979; Wondzell et al. 1996). Grasslands occurred primarily either on level uplands with sandy soils dominated by black grama or on playas or basin floors that received run-in water and were dominated by tobosa grass and burrograss. Shrublands occurred either on sites with shallow, calcareous soils susceptible to water erosion that were dominated by creosotebush (e.g., many upper alluvial fans) or on deep, sandy soils located along stream channels and arroyos that were dominated by honey mesquite.

Currently, most areas are dominated by shrubs with isolated patches of grasslands (Gibbens et al. 2005). The widespread expansion of native shrubs from specific locations into desert grasslands has occurred at unprecedented rates over the past century. This extensive expansion of shrubs has been attributed to a number of interacting factors (chapter 10). Disentangling the role of each factor has proven difficult. However, our landscape model provides new insights and testable hypotheses about the key processes involved and the patterns of expansion. We illustrate this approach for the two most common shrub species in these systems: honey mesquite and creosotebush.

Expansion of honey mesquite plants into grasslands likely occurred through the dispersal of seeds by cattle and small animals. Mesquite pods are palatable and can be dispersed large distances from the seed source (figure 18-5). Establishment and survival of these seedlings occurs frequently. Following this initial establishment, shrub density increases through time as plants fill in an area due to high seed availability (Goslee et al. 2003). Continued grazing by cattle on the few remaining grasses would further reduce

Fig. 18-5. Aerial photo of Camino Real and spatial variation in mesquite *(Prosopis glandulosa)* plants. Most plants are currently found along the original Camino Real established by the Spanish colonizers in the seventeenth century with some dispersal away from the road.

their ability to compete against shrubs. Wind erosion that redistributes fine particles from

bare interspaces to plants would lead to coppice dune formation. These islands of fertility

would result in positive feedbacks to shrub persistence and growth through time. Thus the

key processes involved in mesquite expansion include the widespread seed dispersal by

animals, vegetation–soil–animal feedbacks that negatively affect grasses and promote

shrubs, and wind erosion leading to dune formation and shrub persistence through time.

Expansion by creosotebush into grasslands over the past century was likely

affected by a different set of spatial processes. Creosotebush seeds are relatively large

and unpalatable, thus dispersal was most likely through sheet flow of water or in stream

channels during floods. Constraints on seed germination and seedling establishment of

creosotebush are poorly understood in the Chihuahuan Desert. However, observations

suggest that recruitment events are episodic with large-scale events occurring following

the droughts in the late 1800s and again in the 1950s. Recruitment at this time was likely

promoted by the reduced grass cover due to heavy grazing by cattle over this time period

(Fredrickson et al. 1998). Expansion of this species often occurs in areas where argillic

horizons have been removed by erosion (McAuliffe 1994). Similar to mesquite-

dominated areas, the remaining grasses would be preferentially grazed as shrub density

increases, resulting in positive feedbacks to shrubs with reduced competition from

grasses. Islands of fertility form in creosotebush stands due to water erosion of soil and

nutrients from bare interspaces to plant canopies. Thus, the key processes involved in

creosotebush expansion include localized seed dispersal by water, episodic recruitment

events, and water redistribution at the plant-interspace scale that promotes continued

dominance by shrubs.

Based on these processes, we can predict differences and similarities in the

landscape-scale expansion dynamics of these two shrub species. Creosotebush likely

expanded rapidly over large areas within short periods of time following a large-scale

recruitment event. By contrast, mesquite likely expanded over a longer period of time due

to multiple recruitment events. These statements are supported by the current structure of

the Jornada landscape where mixed stands of honey mesquite and black grama still exist.

Large, monodominant stands of creosotebush or mesquite can be found, but mixed stands

of creosotebush and black grama rarely occur. The fastest expansion for both shrub

species would have occurred on the landscape locations where positive shrub feedbacks

were the strongest or the rates of transfer (seed dispersal, water or wind redistribution)

favoring shrubs were the largest. Some data exist to support this statement; for example,

sites closer to shrublands in the early 1900s converted to shrub dominance faster than

sites farther away (Yao et al. 2002a).

Knowledge gained from studying native shrub expansion using a landscape

perspective can be applied to the current invasion by exotic species or noxious weeds in

many ecosystems worldwide. Most studies of invasive species have focused on species

traits and environmental factors with less attention to biotic feedbacks and landscape

properties (Rejmánek and Richardson 1996; Lonsdale 1999). Based on our work at the

Jornada, identifying key processes, feedbacks, and sensitive parts of the landscape for

different species is necessary for understanding and prediction of these complex

dynamics.

Remediation

Numerous remediation approaches have been attempted since 1912 at the Jornada either

to limit shrub invasion or to return perennial grasses to dominance (chapter 14). Most

attempts have low success rates and poor economic return. Although most remediation

attempts have failed (Rango et al. 2002), there have been enough successes to indicate

that the system can be manipulated (e.g., Cassady and Glendening 1940). In some cases,

it has taken decades for positive effects to become apparent (Rango et al. 2002). Most

remediation attempts in arid and semiarid ecosystems have had limited success for three

major reasons: (1) The key processes limiting vegetation recovery at different spatial and

temporal scales have not been identified, (2) nonlinear thresholds related to vegetation–

soil–animal interactions and feedbacks have been crossed, and (3) the landscape context

and importance of linkages among spatial units within a landscape have been ignored

(Archer 1989; Peters and Betancourt 2001). Our landscape perspective has the potential

to overcome these limitations and provide new insight and prediction into remediation

efforts.

High spatial and temporal variability inherent in arid and semiarid ecosystems has

led to the failure of many remediation attempts. However, this natural variability across a

landscape and through time can be used to our advantage (Landres et al. 1999). Using our

landscape perspective, the potentials and limits of different parts of a landscape as well as

the key processes affecting ecosystem dynamics can be identified. This approach also

allows us to take advantage of extreme events, such as El Niño and drought, which

interact with different parts of a landscape differently. In particular, we can focus on

landscape locations where vegetation–soil–animal processes and landscape context are

important in generating nonlinear dynamics (Illius and O'Connor 1999; Holmgren and

Scheffer 2001), thus increasing the probability that an extreme event will produce a

positive result. Prioritizing efforts by concentrating on locations likely to change under

certain conditions and focusing on key processes will provide guidelines and

recommendations for future remediation efforts (Herrick et al. 1997).

Carbon and Nutrient Dynamics

Carbon sequestration and dynamics in arid and semiarid ecosystems have become an

increasingly important issue relative to the global carbon budget. Recent estimates of

carbon sinks in the coterminous United States from 1980 to 1990 indicate that grasslands

and shrublands may account for similarly large amounts of carbon storage as forests

(Pacala et al. 2001). Shrub-dominated ecosystems are important contributors to carbon

sinks as a result of their extensive area (44% of the total land area) and their large

potential rates (Hibbard et al. 2001; Pacala et al. 2001). Increases in above- and

belowground carbon storage as well as increases in emissions of NO_x and nonmethane

hydrocarbons (e.g., terpenes, isoprene, and other aromatics) have resulted from the

replacement of grasses by shrubs (Archer et al. 2001; Pacala et al. 2001; Jackson et al.

2002).

Although the total or average amount of carbon sequestered by grasslands and

shrublands is of interest at the global scale, the spatial distribution and temporal dynamics

of carbon across landscapes is of more interest and concern to land managers (Bird et al. 2002; Breshears and Allen 2002). Spatial patterns in carbon and other soil nutrients across landscapes may be complex due to processes such as wind and water erosion, disturbance, and animal redistribution of plant material and nutrients (Schlesinger and Pilmanis 1998). The redistribution of carbon and soil nutrients across a landscape may be as important to vegetation dynamics as local inputs, especially for nitrogen (chapter 6). Thus, incorporating these transfers of materials among spatial units is necessary to understand and predict carbon and nutrient dynamics for landscapes .

Most estimates for carbon sinks and losses have a high degree of uncertainty due to landscape-scale variation in edaphic and topographic factors (Schlesinger and Pilmanis 1998; Pacala et al. 2001; Hurtt et al. 2002). Providing estimates of carbon dynamics based on an average value for a landscape may be misleading. Some vegetation types will have extremely high standing biomass and production, whereas other types will have very low values (Huenneke et al. 2002). Weighting by the area covered by each type would improve the accuracy of the overall estimate, but spatial as well as temporal variation within each type will still not be accounted for. Thus, estimates based on relatively few samples that are extrapolated to the landscape likely misrepresent the values obtained by sampling locations with extreme values and accounting for transfers of materials among spatial units.

Conclusions

Decades of research at the Jornada through the ARS, New Mexico State University, and the LTER have provided a wealth of information on many aspects of arid and

semiarid systems. However, a number of pressing problems and perplexing issues still remain. High spatial and temporal variation in ecosystem dynamics across multiple scales cannot be explained using current models of these systems (e.g., Schlesinger et al. 1990). We developed an interactive landscape model that incorporates three key properties of landscapes: (1) feedbacks among plants, animals, and soils; (2) contagious processes that generate fluxes and flows within and among spatial units; and (3) landscape characteristics, including structure and spatial configuration of spatial units as well as the characteristics of the study area or its context relative to its surroundings. This landscape scale perspective provides new insight into old problems (i.e., shrub invasion, remediation) and an operational approach to deal with new problems, such as carbon dynamics and global climate change. Thus, perspective is central to our long-term efforts as the first century of research is completed in the Jornada Basin and we look toward the next decades of the twenty-first century.