Variation in ecological resilience: a fundamental concept for rangeland ecology

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1973-1989

RESILIENCE AND STABILITY OF ECOLOGICAL SYSTEMS

❖ 4050

C. S. Holling
Institute of Resource E

INTRODUCTION

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Nature Vol. 269 6 October 1977 471

review article

Thresholds and breakpoints in ecosystems with a multiplicity of stable states

Robert M. May*

Theory and observation indicate that natural multi-species assemblages of plants and animals are likely to possess several di simple 1- and 2-s human host–para

Ecological Monographs, 57(1), 1987, pp. 1–21
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EQUILIBRIUM AND NONEQUILIBRIUM CONCEPTS IN ECOLOGICAL MODELS[1]

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Abstract. Mathematical models and empirical studies have revealed two potentially disruptive influences on ecosystems: (1) instabilities caused by nonlinear feedbacks and time-lags in the interactions of biological species, and (2) stochastic forcings by a fluctuating environment. Because both of these phenomena can severely affect system survival, ecologists are confronted with the question of why complex ecosystems do, in fact, exist. Our study analyzes the basic themes of this research and identifies five general hypotheses that, in recent years, theoretical ecologists have built into models to increase their stability against disruptive feedback and stochasticity. To counter feedback instabilities, theoreticians have considered (1) functional interactions between species that act as stabilizers, (2) disturbance patterns that interrupt adverse feedback effects, and (3) the stabilizing effect of integrating small-spatial-scale systems into large landscapes. To decrease the influence of stochasticity, modelers have hypothesized (4) compensatory mechanisms operating at low population densities, and (5) the moderating effect of spatial extent and heterogeneity. We show that modeling based on these ideas can be organized in a systematic way. We also show that the stable equilibrium state should not be viewed as a fundamental property of ecological systems, but as a property that can emerge asymptotically from extrapolation to sufficiently large spatial scales.

Key words: *ecological stability; mathematical models; nonequilibrium; spatial heterogeneity; species persistence; stochastic; temporal and spatial scales.*

Introduction

Models are abstractions of how we think nature operates. The premise that there is a "balance of nature" has been a tradition in Western thought dating back to antiquity. This premise was taken up uncritically by many natural historians as ecology came of age as a science during the last few centuries (Egerton 1973), and has permeated efforts to model ecological systems mathematically. Models have usually been structured on the basis of a community of species in an ecosystem having an equilibrium state. ("Steady state" is a more appropriate term than "equilibrium," but we will use the latter term, keeping in mind that it means a "dynamic equilibrium.") This classical view admits that species can deviate from equilibrium, and that the equilibrium state may be unstable in many cases, giving rise to population oscillations about it. Nonetheless, this view attaches fundamental significance to there being such an equilibrium state. We will refer to this as the "equilibrium view" in mathematical ecology, (Rosenzweig and MacArthur 1963), the Nicholson-Bailey model (Nicholson 1933, Nicholson and Bailey 1935), and their many variations, all of which have well-defined mathematical equilibrium points.

The equilibrium view of ecological systems, which has always had a fair number of skeptics, now seems unsatisfactory to a large fraction, perhaps a majority, of ecologists. This dissatisfaction, expressed clearly by Reddingius (1971), Caswell (1978), Murdoch (1979), Connell and Sousa (1983), and Wiens (1984*a*), among others, does not hinge on the mere question of system stability, but on whether it is valid to define the existence of an equilibrium state at all, stable or unstable. The existence of such a population or community equilibrium state requires the assumption of density-dependent population growth, which is often unestable. In addition, a practical difficulty with models based on the assumed existence of an equilibrium state is that they cannot be extrapolated down to small spatial scales on which observations are often made. For example,

Opportunistic management for rangelands not at equilibrium

MARK WESTOBY, BRIAN WALKER, AND IMANUEL NOY-MEIR

Abstract

We discuss what concepts or models should be used to organize research and management on rangelands. The traditional range succession model is associated with the management objective of achieving an equilibrium condition under an equilibrium grazing policy. In contrast, the state-and-transition model would describe rangelands by means of catalogues of alternative states and catalogues of possible transitions between states. Transitions often require a combination of climatic circumstances and management action (e.g., fire, grazing, or removal of grazing) to bring them about. The catalogue of transitions would describe these combinations as fully as possible. Circumstances which allow favorable transitions represent opportunities. Circumstances which threaten unfavorable transitions represent hazards. Under the state-and-transition model, range management would not see itself as establishing a permanent equilibrium. Rather, it would see itself as engaged in a continuing game, the object of which is to seize opportunities and to evade hazards, so far as possible. The emphasis would be on timing and flexibility rather than on establishing a fixed policy. Research under the state-and-transition model would aim to improve the catalogues. Frequencies of relevant climatic circumstances would be estimated. Hypotheses about transitions would be tested experimentally. Often such experiments would need to be planned so that they could be implemented at short notice, at an unknown future time when the relevant circumstances arise.

Key Words: equilibrium, climax, succession, models

Applied ecology disciplines such as range management necessarily are organized around a model as to how their ecosystem functions. By a model we mean a system of concepts, generalizations, or assumptions. The model guides what data are collected, and how that information is assembled so as to arrive at management decisions. This paper discusses the choice of models for managing rangelands. The discussion will contrast 2 clearly distinct models which we will call the "range succession model" and the "state-and-transition model". However it should be understood that these represent 2 ends of a spectrum of possibilities. By contrasting the extremes, we hope to bring out the issues clearly.

Up to the present most range managers have been taught concepts much closer to the range succession model than to the state-and-transition model (Lewis 1969, Tueller 1973, Heady 1975, Stoddart, Smith and Box 1975, Smith 1988). The range succession model has not gone unchallenged. On the contrary, a number of range scientists have criticised it. The main criticisms are summarized later. However, despite the scientific criticisms, most management continues to be organized by reference to the range succession model.

Accordingly our purpose in this paper is not to criticise the range succession model further at the level of scientific evidence or theory, but rather to develop alternative ways of formulating existing knowledge for purposes of management. The state-and-transition model is the alternative we consider. We discuss how research and management would be affected if the state-and-transition model were to be widely used instead of the range succession model.

The Range Succession Model

The successional approach to range management derives from Clementsian ideas of plant ecology (Clements 1916, Weaver and Clements 1938, Tobey 1981). It was suggested very early (Sampson 1917, 1919). US government agencies developed it into a practical system of range classification. In the 1940's and 1950's it became firmly established as the consensus of the range management profession, expressed in the first 2 editions of Stoddart and Smith (1943, 1955), in the masterly review by Ellison (1960), and in a series of conceptual papers in the journals of the profession (Humphrey 1945; Dyksterhuis 1949, 1958; Parker 1954; Hanson 1957).

The model supposes a given rangeland has a single persistent state (the climax) in the absence of grazing. Succession towards this climax is a steady process. Grazing pressure produces changes which are also progressive and are in the opposite direction to the successional tendency. Therefore the grazing pressure can be made equal and opposite to the successional tendency, producing an equilibrium in the vegetation at a set stocking rate. A sustainable yield of livestock products can be harvested from such an equilibrium. All possible states of the vegetation can be arrayed on a single continuum (Fig. 1a) from heavily-grazed, early-successional, poor condition, to ungrazed, climax, excellent condition. Condition is the technical term for the vegetation's position on this continuum. Trend is the term for the vegetation's travel along the continuum. Much research effort has been devoted, and still is, to developing methods for assessing and monitoring condition and trend on particular rangelands. Under the range succession model the object of management is to choose a stocking rate which establishes a long-term balance between the pressure of grazing and the successional tendency.

The model recognizes that vegetation is affected when rainfall varies from year to year. A balance between the pressure of grazing and the successional tendency of the vegetation can not produce a completely unvarying equilibrium. The range succession model deals with varying rainfall by supposing that drought affects vegetation in a similar way to grazing, and conversely that above-average years have effects which can be understood as accelerating the successional tendency (Fig. 1b). Therefore, under the range succession model, management should respond to drought by reducing grazing pressure, so that the combined pressure of drought and grazing varies as little as possible, the balance of these combined pressures with the successional tendency is maintained, and the position of the vegetation on the condition scale is stabilized.

Under the range succession model research and management proceed as follows. Resource inventory classifies and maps rangelands according to their climax-type, and within each climax-type, according to current condition. Grazing trials determine whether range condition improves or deteriorates from various condition classes at various stocking rates (Fig. 2, arrows). These trials

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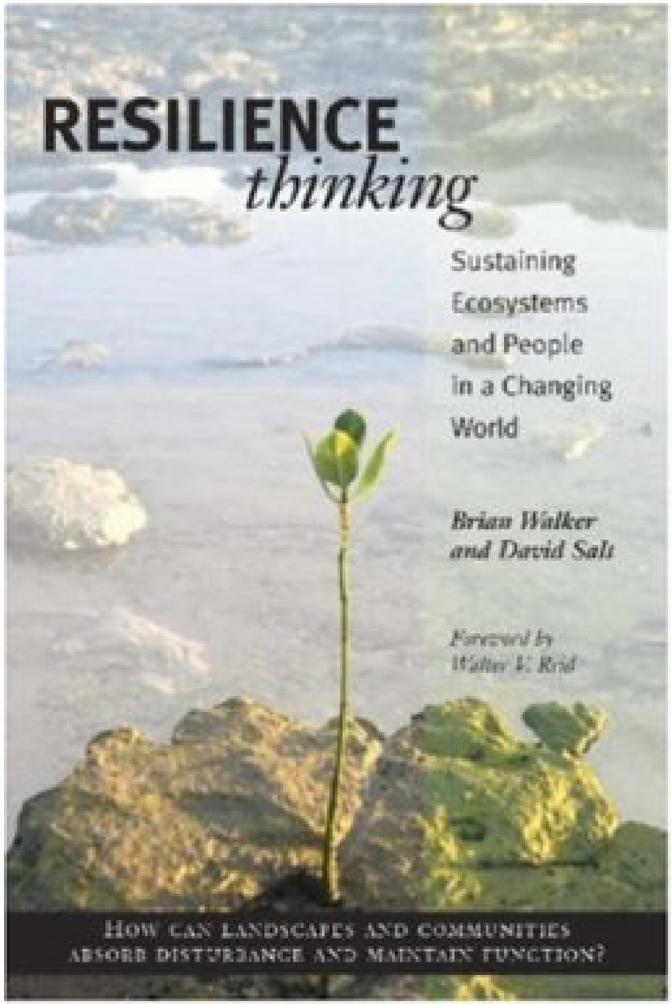
2000-present



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Ecological Resilience—in Theory and Application

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LETTER

Rising variance: a leading indicator of ecological transition

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Abstract

INTRODUCTION

Regime shifts are substan complex systems such as (Steele 1998; Scheffer *et al* 2002; Carpenter 2003; Fol 2004; Brock *et al.* 2006; F Brock 2006). In ecology, include eutrophication of among grassy and wood degradation of coral ree (Scheffer *et al* 2001; Fo control key system proce shift (Holling 1973). For water) lakes the concent primary production are co the watershed, whereas concentrations of nutrien the lake as well as inputs feedback changes are kn types of ecosystems (Sch

REVIEW

Self-Organized Patchiness and Catastrophic Shifts in Ecosystems

Max Rietkerk,[1*] Stefan C. Dekker,[1] Peter C. de Ruiter,[1] Johan van de Koppel[2]

Unexpected sudden catastrophic shifts may occur in ecosystems, with concomitant losses or gains of ecological and economic resources. Such shifts have been theoretically attributed to positive feedback and bistability of ecosystem states. However, verifications and predictive power with respect to catastrophic responses to a changing environment are lacking for spatially extensive ecosystems. This situation impedes management and recovery strategies for such ecosystems. Here, we review recent studies on various ecosystems that link self-organized patchiness to catastrophic shifts between ecosystem states.

Ecosystems are exposed to changes in climate, nutrient loading, or biotic exploitation. How ecosystems undergo such environmental changes on different scales of space and time is one of the main frontiers in ecology. Although environmental change can be slow and gradual, it may lead to sudden catastrophic change in the structure and functioning of ecosystems (*1*). Such catastrophes are commonly attributed to the existence of two alternative stable states in ecosystems (*2*), meaning that the dynamics of these systems are determined by two attracting states. Here, we define this as bistability.

Positive feedback control between consumers (e.g., plants) and limiting resources (e.g., water, nutrients) is considered to be the principle underlying catastrophic ecosystem shifts (*1*–*3*). This picture emerged from models that ignore spatial interactions. Hence, these so-called mean field models predict bistability in ecosystems as a consequence of positive feedback. We interpret this as local bistability. Such mean field analysis is particularly helpful for understanding catastrophic shifts in homogeneous or well-mixed ecosystems. The sudden loss of transparency in shallow lakes provides an illustrative example (*4*, *5*). However, verifications and predictive power of catastrophic shifts are lacking for spatially extensive, heterogeneous ecosystems. As a result, sustainable management and recovery strategies for such ecosystems have been difficult to devise; they require an understanding of the relation between feedback and spatial scale.

We review recent ecosystem studies that include feedback control and spatial scale (Table 1 and Fig. 1). These studies link feedback control to self-organized patchiness of consumers and resources, and they show that a resource concentration mechanism invoked by consumers explains the diversity of spatial structures in these ecosystems. Such consumers have previously been called "ecosystem engineers" (*6*). Spatial self-organization is not imposed on any system but emerges from fine-scale interactions owing to internal causes (*7*). Moreover, model outcomes show that ecosystems where this resource concentration mechanism operates exhibit bistability between a specific spatially structured and homogeneous ecosystem state. We define the bistability at large spatial scales predicted by these spatially explicit models as global bistability.

Similar to the mean field models, global bistability in spatially explicit models is associated with catastrophic shifts at large spatial scales between coexisting stable states. Hence, these results stress the importance of self-organized patchiness for a better understanding of catastrophic shifts. Increased resource scarcity leads to spatial reorganization of consumers and resources in these model ecosystems, and an ecosystem state develops with localized structures observed in reality. Once resource scarcity reaches a threshold, the system shifts toward a homogeneous state

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Table 1. Overview of references describing self-organized patchiness in some major ecosystems and the mechanisms involved.

Ecosystem	References	Pattern characteristics (scale)	Mechanisms involved
Arid	(*8*, *11*)	Spots, labyrinths, gaps (1 m) and stripes (10 m) (Fig. 1C)	Redistribution of soil water due to positive feedback among plant biomass, extent of root system, and water uptake
	(*9*, *14*)	Periodic spots and bands (10 to 100 m)	Short-range facilitation and long-range competition for limiting water
	(*12*)	Spots, labyrinths, gaps, and stripes (10 to 100 m) (Fig. 1, A and B)	Redistribution of surface water due to positive feedback between plant cover and water infiltration
	(*13*)	Disordered spots and clustered spots on hillslope contours (10 to 100 m)	Competition for limiting water
Savanna	(*15*)	Isolated spots of trees and shrubs in grass matrix (10 to 100 m) (Fig. 1, D and E)	Short-range facilitation and long-range competition for limiting nutrients
Peatland	(*24*)	String patterns (10 m)	Ponding of surface water upstream from hummocks combined with positive feedback between hummock occurrence and water table depth
	(*25*)	Maze and string patterns perpendicular to flow direction (10 m) (Fig. 1, F and G)	Convective transport of limited nutrients in the groundwater toward areas with higher plant biomass, driven by differences in transpiration rate

Structure of talk

1. Review 6 concepts in “resilience theory” that we feel are especially relevant to the production of state-and-transition models for rangelands.

2. How the concept improves models and management

3. Provide examples from rangelands.

Concept 1: Resilience

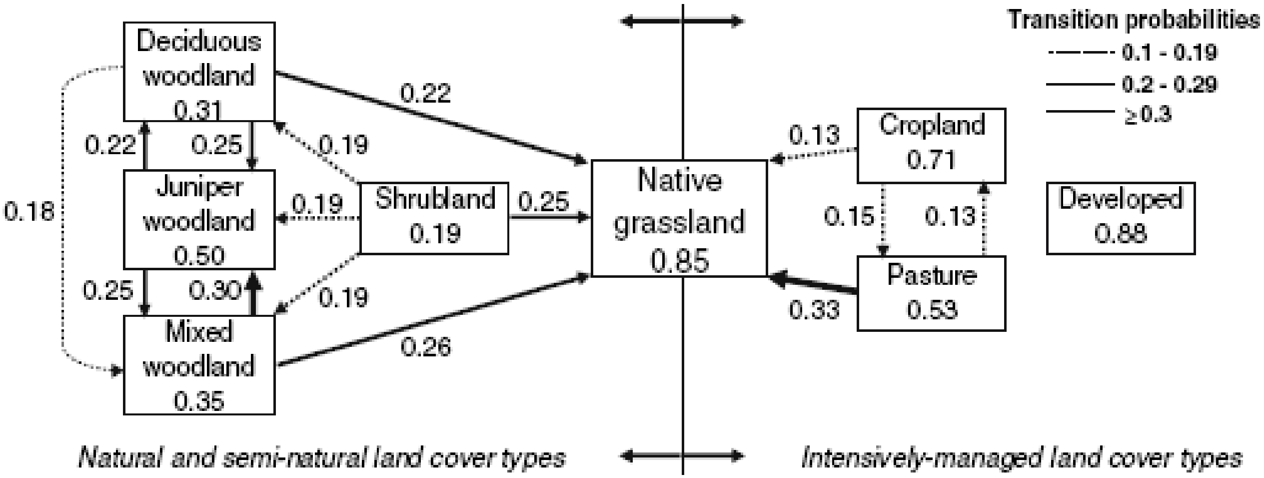
Engineering resilience: how quickly a system returns to equilibrium (e.g., within a state)

Ecological resilience: capacity of a system to absorb a disturbance without fundamental changes to its characteristic processes and feedbacks (i.e., to a new equilibrium, a new state)

Importance: distinguishes two key aspects (and approaches) for state-and-transition models

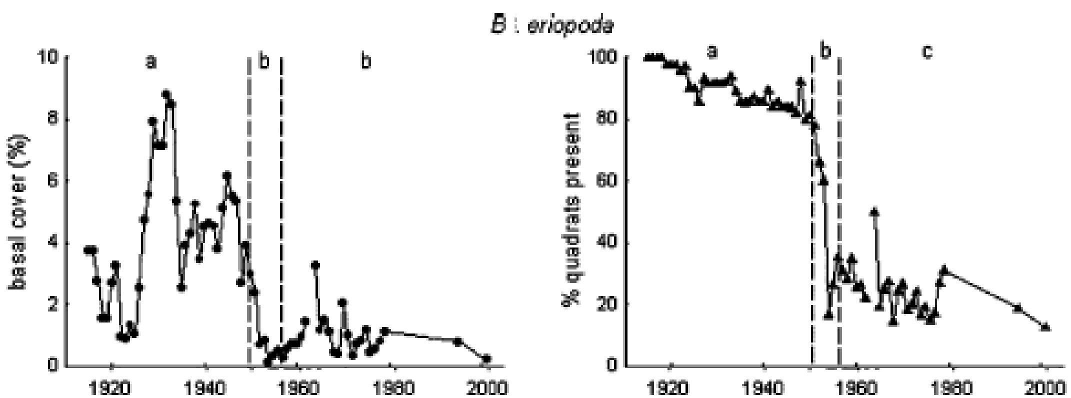
Concept 1: Resilience

a. Rates of change/recovery for community types in southern plains grassland



Coppedge et al., 2007
Landscape Ecology 22: 1383

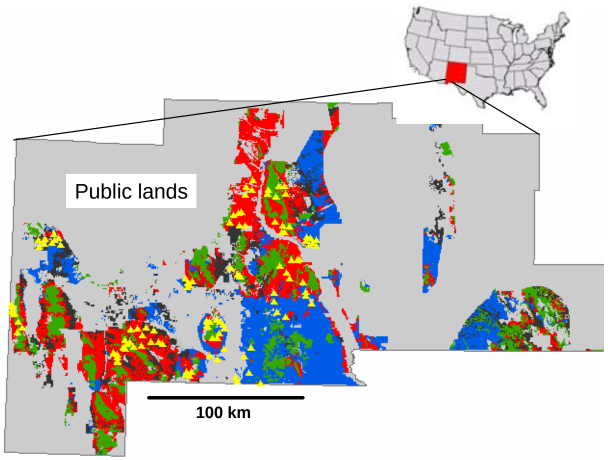
b. Drought-induced shift in state in Chihuahuan desert grassland



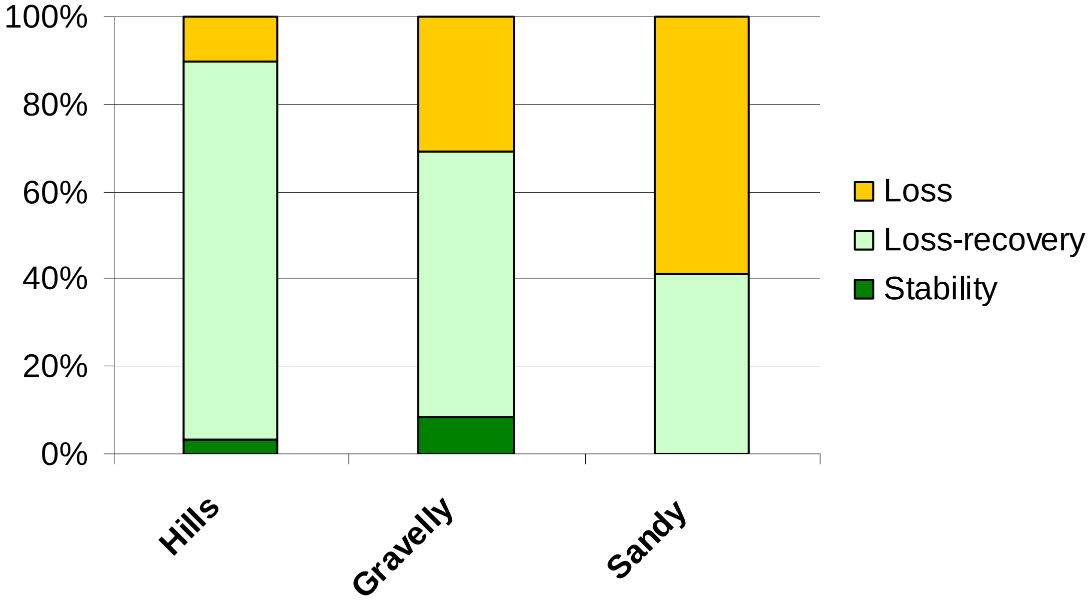
Yao et al., 2006
Landscape Ecology 21: 1217

Concept 1: Resilience

Ecological resilience varies spatially at several scales

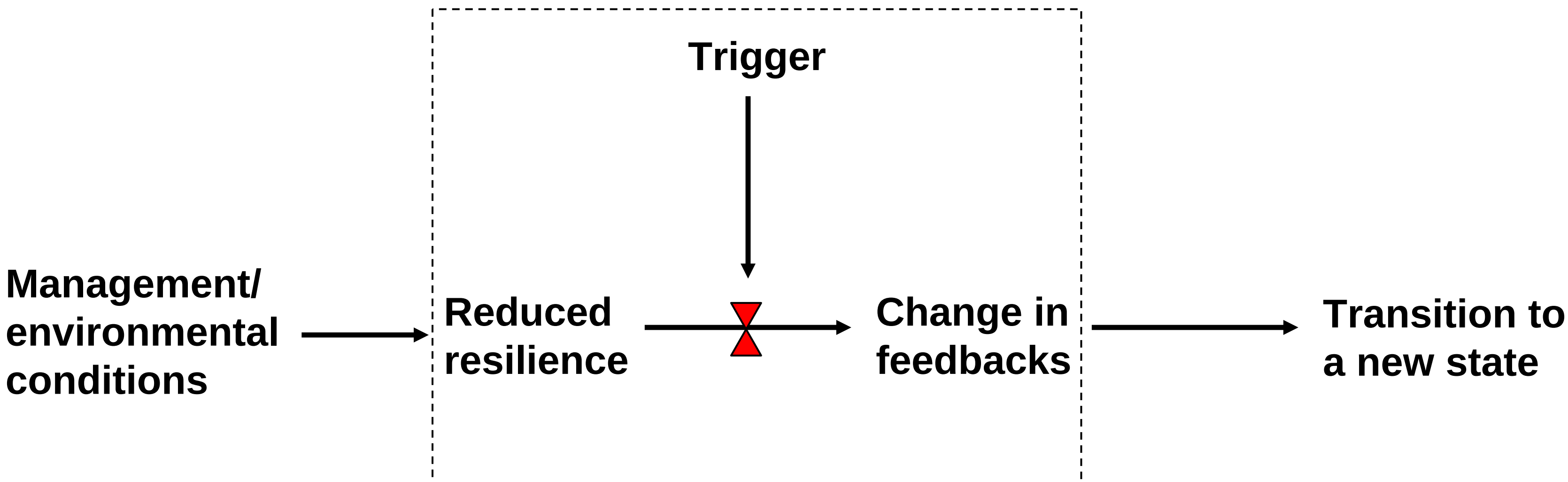


Grass dynamics in 123
trend plots: ca. 1970-2003



Concept 2: Thresholds or tipping-points

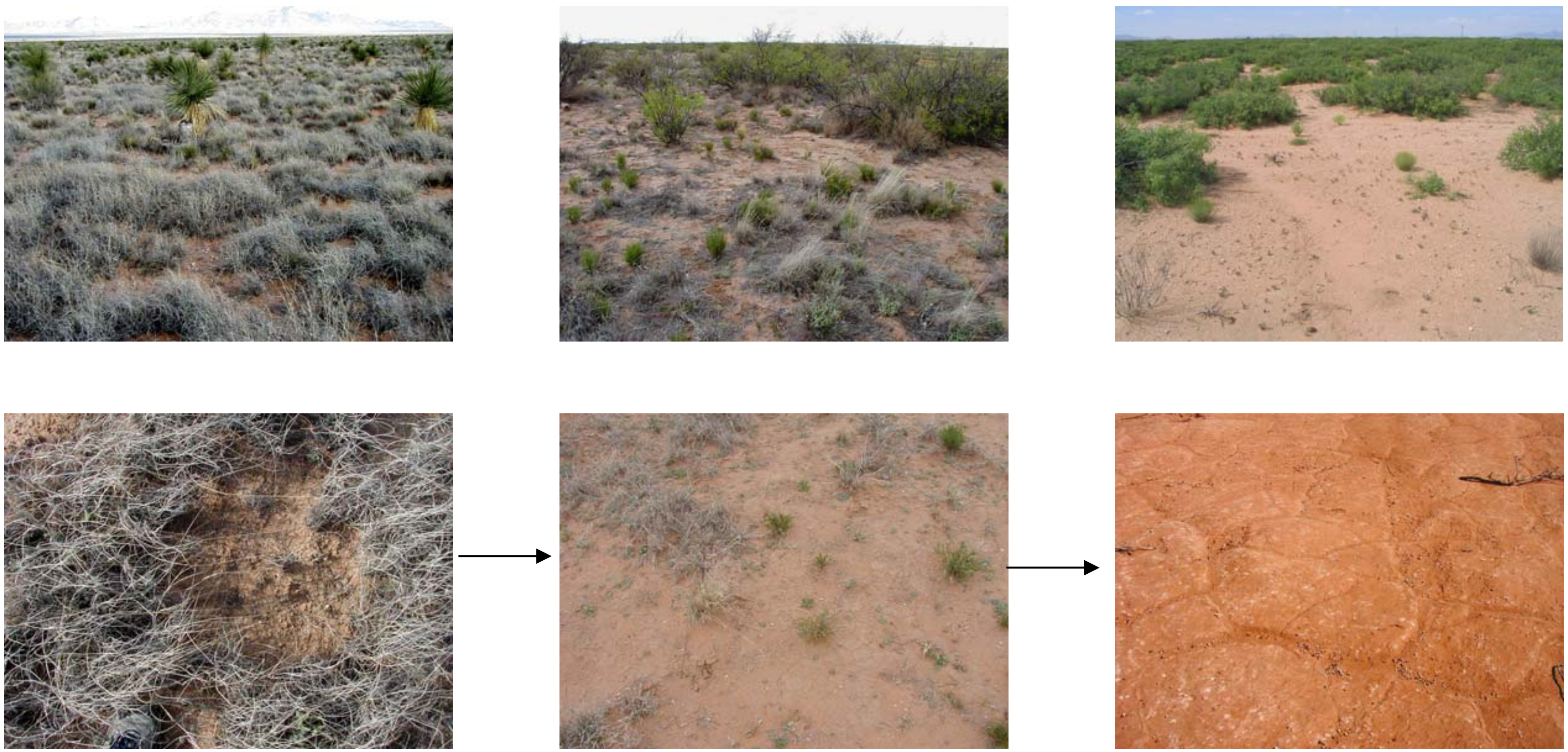
Mechanisms by which resilience is lost and a transition occurs, usually related to changes in feedback systems.



Importance: provides an operational concept for anticipating and mitigating the persistent loss of desired services

Concept 2: Thresholds or tipping-points

Increasing bare ground connectivity is a key measurement in arid rangelands



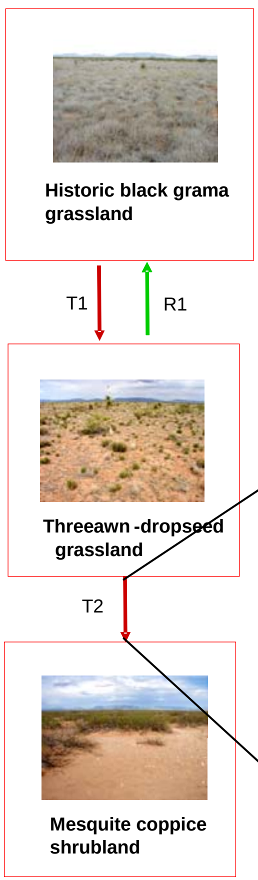
Pre-threshold state, resilient condition

Pre-threshold state, reduced resilience

Post-threshold state

Concept 2: Thresholds or tipping-points

Threshold decomposition: there are distinct stages of development of a threshold



Pattern/structure (vulnerability) → ***Indicators of management needs***
(e.g., bare ground connectivity)

↓

Process (feedback) → ***Indicators of management needs***
(e.g., erosion rate)

↓

Degradation (irreversibility) → ***Indicators of restorability***
(e.g., topsoil depth and water-holding capacity)

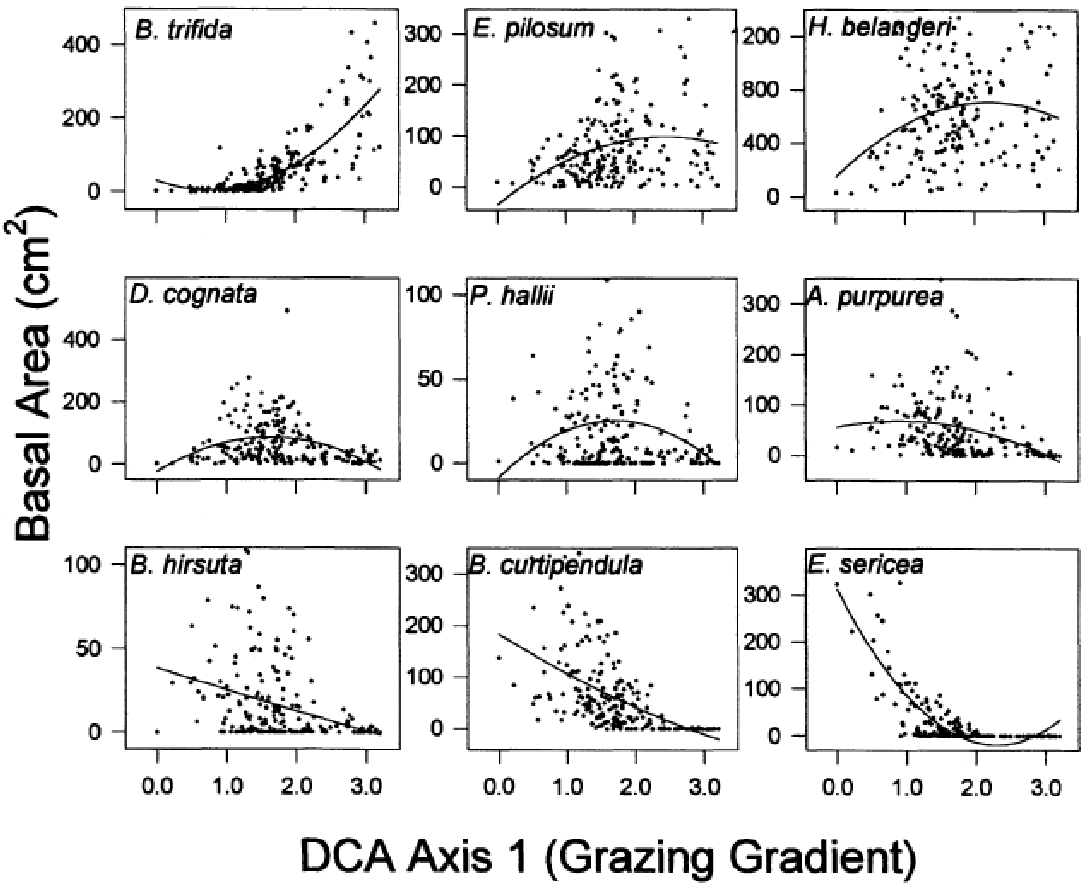
Concept 3: Functional vs. response diversity

Functional diversity: variety of organisms that support distinct ecosystem functions

Response diversity: variety of responses to environmental change among species that contribute to the same ecosystem function (i.e., redundancy).

Importance: High response diversity promotes resilience, systems that exhibit low redundancy and vulnerable species have inherently low resilience.

Concept 3: Functional vs. response diversity



Fuhlendorf and Smeins 1997
Journal of Vegetation Science
8: 819

Response diversity in Texas savanna,
grazing-tolerant species stabilize grassland state

Concept 3: Functional vs. response diversity

1993

2004

Once black grama grass is gone, dropseed grass cannot stabilize soil in drought

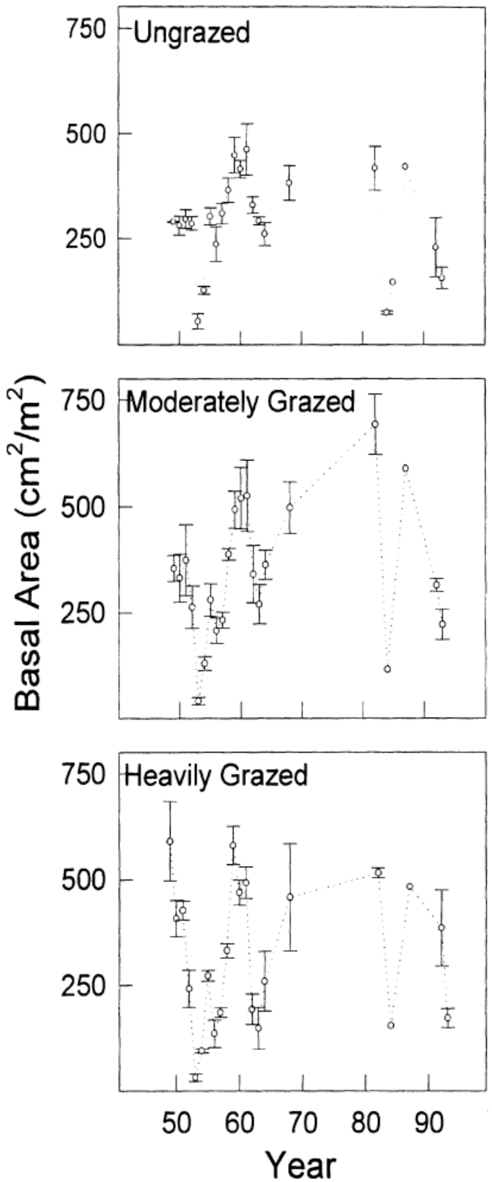
Concept 4: Slow vs. fast variables

Slow variables: factors that change slowly in response long-term processes and that constrain responses of fast variables.

Fast variables: factors that change rapidly and that are most easily measured by managers

Importance: Slow variables determine the resilience of an ecosystem

Concept 4: Slow vs. fast variables



Fast variable: Grass cover

- Often the focal variable for managers
- Difficult to ascertain loss of resilience due to high variability

Fuhlendorf et al., 2001
Applied Vegetation Science 4: 177

Concept 4: Slow vs. fast variables

Slow variable: Fill-in and growth of trees to fire-resistant condition

1964

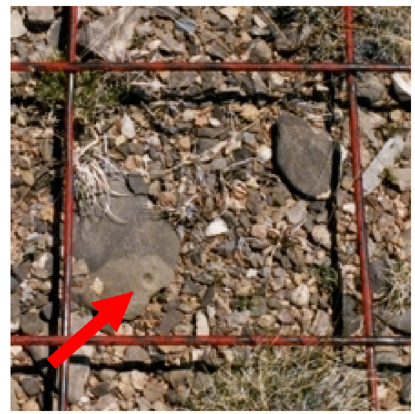
2002

Concept 4: Slow vs. fast variables

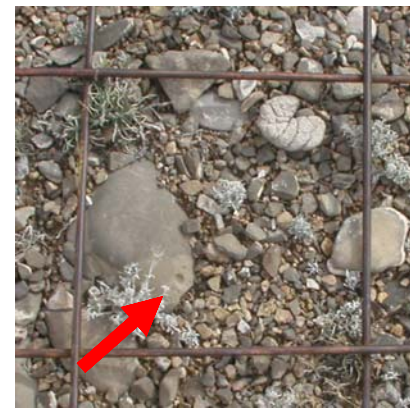
Slow variable: Gradual soil deflation and reduced WHC in juniper savanna

1969

1979



1993



2005

Measurement of slow variables often requires techniques that differ from those used to measure fast variables

Concept 5: Cross-scale interactions

Processes at one scale interact with those at other scales to determine thresholds

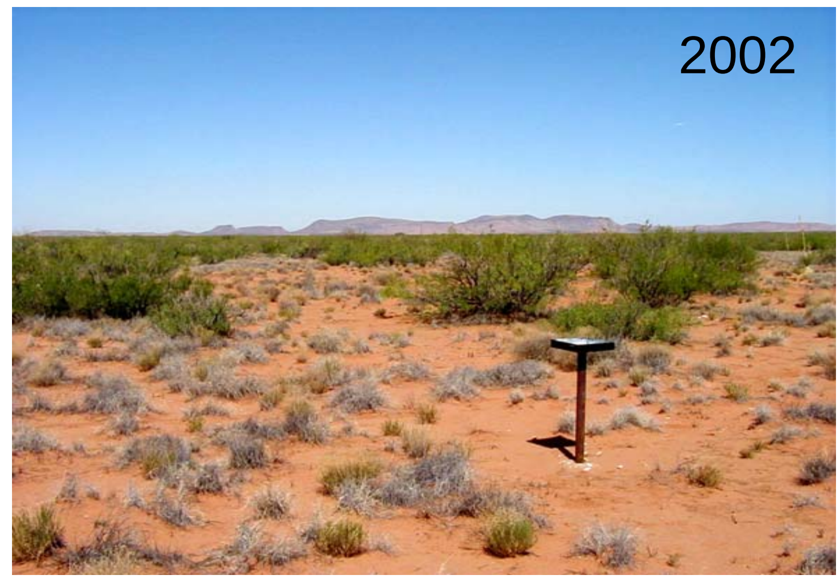
Importance: Observations at multiple scales are needed to interpret rangeland change. The scale driving rangeland dynamics may change over time

We often ignore the landscape context of our observations

Concept 5: Cross-scale interactions

Grazing exclosure--1950

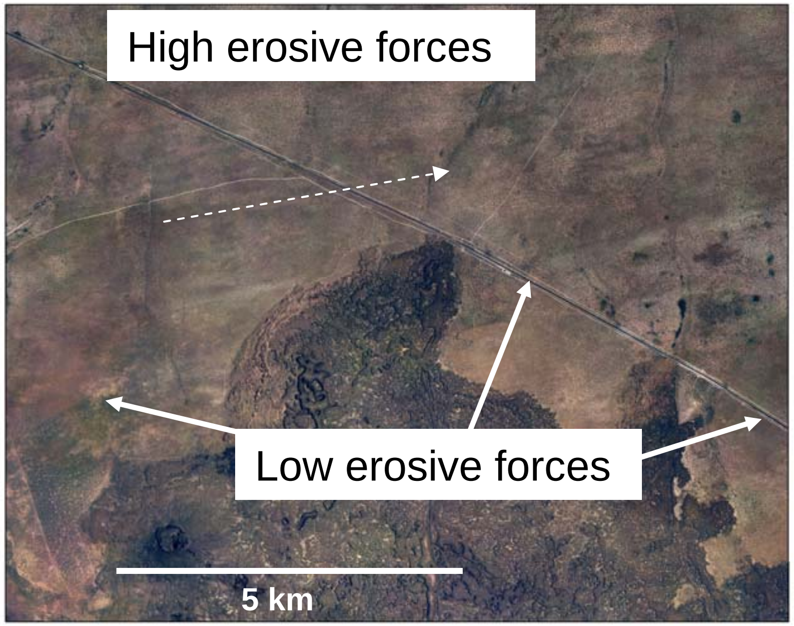
1961

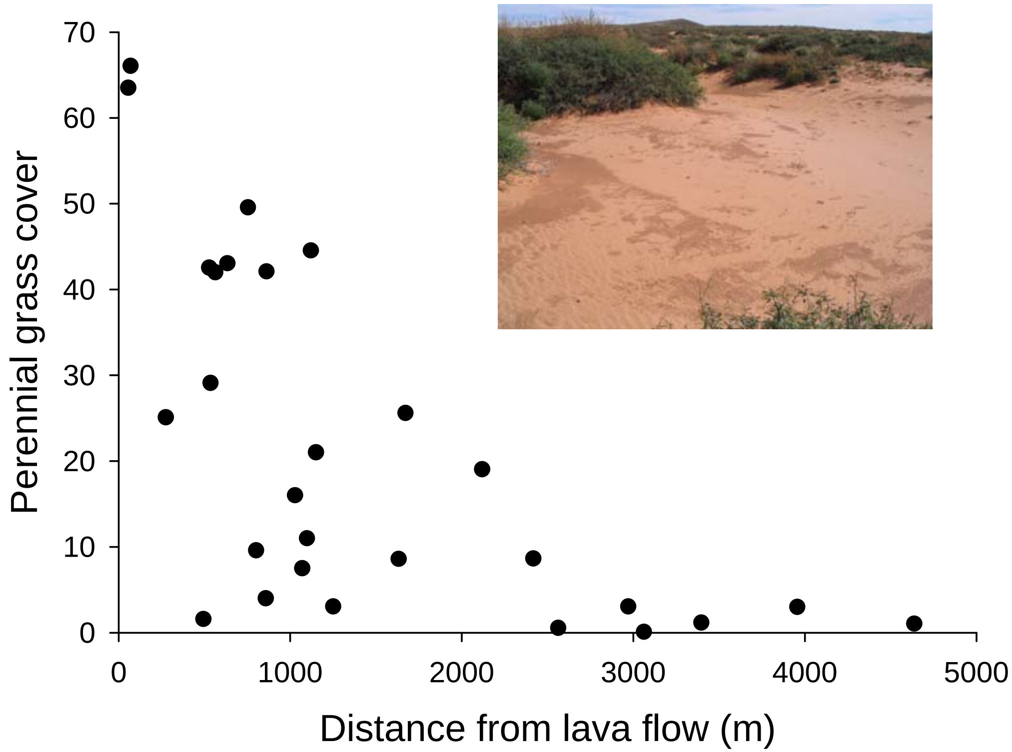


Broad-scale drivers overwhelm local management interventions

Concept 5: Cross-scale interactions

All are similar loamy sand soils





Remnant grasslands determined in part by cross-scale interactions

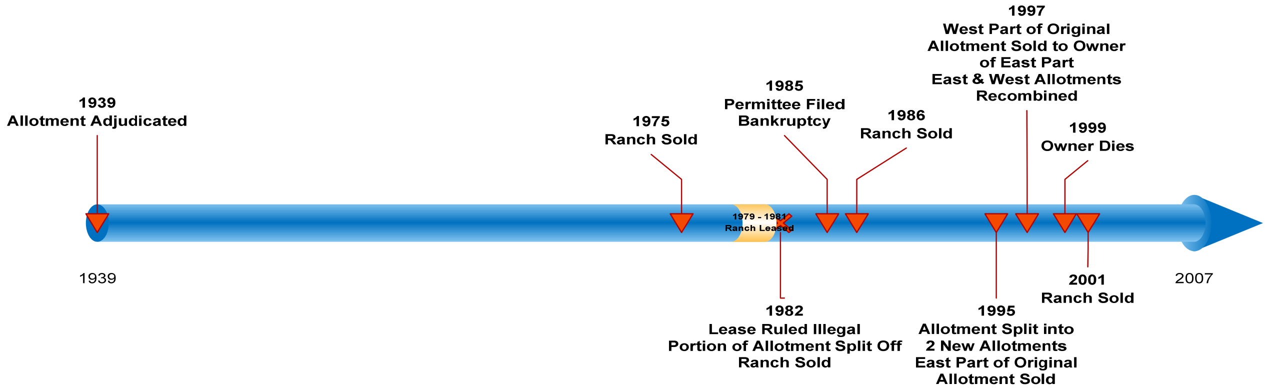
Concept 6: Social-ecological systems

The feedback between human decision-making and ecological processes ultimately determines ecological resilience

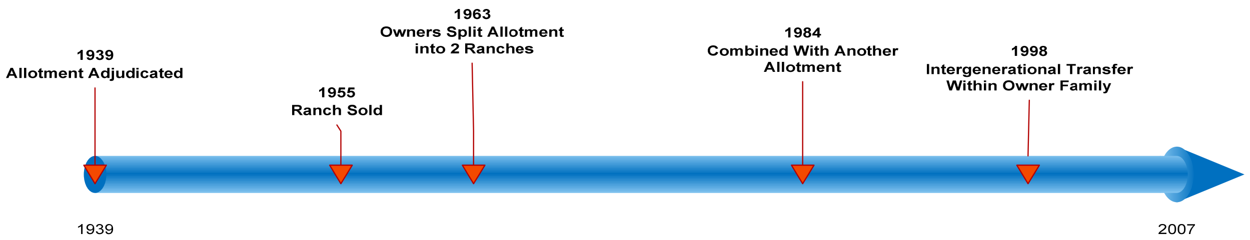
Importance: We need a better understanding of how ranching livelihoods are linked to environmental conditions to effectively use state-and-transition models

Concept 6: Social-ecological systems

Sandy (low resilience) allotment



Gravelly/Hills (high resilience) allotment



We may need different recommendations/policies for different sites and regions

Conclusions: key themes for state-and-transition models and research

- Describe how both engineering and ecological resilience varies among ecological sites.
- Indicators of a) threshold initiation, b) feedbacks, and c) persistent degradation
- Better characterization of key slow variables in models
- Descriptions of how species biology/community interactions determine resilience.
- Consider possibility of cross-scale feedbacks and the need for landscape-scale indicators
- Document human-environment interactions with respect to ecological sites