Overview of landscape dynamic concepts

Instructor: K. McGarigal

Assigned Reading: Turner et al. 2001 (Chapter 7); Sprugel (1991)

Objective: Provide an overview of important concepts underpinning the study of landscape dynamics and alternative concepts of landscape equilibrium. Highlight the spatial and temporal scaling of disturbance regimes and the influence on equilibrium/nonequilibrium dynamics.

Topics covered:
1. Landscape dynamics concepts – stability, persistence, resistance, resilience and recovery
2. Landscape equilibrium concepts – absolute constancy, shifting mosaic-steady state, stationary processes, bounded equilibrium
3. Nonequilibrium landscapes – role of legacies, landscape uniqueness, importance of scale
4. Disturbance and landscape equilibrium – scaling of disturbance regimes
5. Anthropogenic influences on landscape dynamics
6. Management implications

Comments: Some material taken from Dean Urban’s Landscape Ecology course notes

13.1
1. Landscape Dynamics Concepts

For heuristic purposes, a simple conceptual framework for discussing ecosystem/landscape dynamics is needed. In this simple model, we depict system dynamics as a trajectory over time in a state variable. A state variable is any variable that describes the state or condition of the system at a single point in time and is typically a measure of system structure or function. For example, the percentage of the landscape in a particular vegetation condition, mean patch size, total water discharge, and net primary productivity are all examples of potential state variables. As shown here, under a “natural” disturbance regime, the trajectory in a state variable might fluctuate over time in response to disturbance and succession processes and vary within a “natural range of variability”, or what is sometimes referred to as the “normal multiple states operating range”. Note, this range of variability is relative to a specific spatial and temporal scale.
This model provides a simple reference framework for assessing the effects of human activities on system dynamics. For example, in this figure, two alternative human-altered trajectories are depicted, and we might ask whether the system depicted by each trajectory is “healthy” in reference to the natural range of variability. In both cases, the system dynamics are substantially modified; specifically, the dynamics are substantially dampened. In the one case, the system remains within its natural range of variability, while in the other case, the system moves to an equilibrium state outside of its natural range of variability. In both cases, we might ask whether the trajectory depicts a “healthy” system. This is not an easy question to answer in either case.
Any consideration of system dynamics automatically invokes issues of scale because the range of variability in any state variable can only be defined in reference to a specific spatial and temporal scale. For example, as the spatial extent of the system gets larger and larger (i.e., coarser scale), the expected range of variability is likely to decrease as the system increasingly is able to incorporate the disturbances; i.e., balance of disturbance against succession (sensu Watt’s unit pattern).
Defining this scaling relationship for a natural system is of interest to us of course, but perhaps of even greater interest is how this scaling relationship changes under a human-modified disturbance regime. For example, if the human-altered trajectory looks like the one depicted here (i.e., the range of variability is increasingly dampened as the spatial scale increases), we might ask whether this is a healthy system?
Understanding system dynamics has utility in a wide range of applications. For example, a question of great importance to resource managers is whether recent trends in wildlife populations and/or habitat are biologically significant and signal the need for corrective management action. If the trajectory is decreasing (e.g., population decrease), for example, managers are often quick to interpret this as a signal for immediate management action. However, an understanding of system dynamics may reveal that the decrease is perfectly natural and well within the range of natural variation.
And as we have already discussed, a quantitative understanding of system dynamics can be vitally important in providing a reference framework for interpreting measures of landscape structure. Recall that it is often difficult, if not impossible, to determine the ecological significance of the computed value of a landscape metric without understanding its natural range of variability.
In ecology, many terms have been defined to explain the state of a system over time, how readily that system state changes, and the trajectory of change in response to a disturbance or perturbation. Of course, identifying system state changes requires identifying state variables that are descriptive of the system state. Unfortunately, it is extremely difficult to identify state variables that are sensitive to fine-scale changes in ecosystem states and that can be used by managers to detect system changes due to a management activity, although we will explore some useful measures later.

A number of system descriptors serve as organizing concepts for the study of systems dynamics.

- **Stability**—The tendency of an ecosystem to move away from a stable state. In the case of ecological systems (which are highly dynamic), stability refers not to stasis of all state variables but to variations within some defined bounds. Instability results when the system crosses some threshold from which recovery to a former state is either impossible (e.g., extinction) or, if possible, occurs only over relatively long periods of time or with considerable subsidies of energy and matter (e.g., loss of topsoil).

- **Persistence**—The length of time an ecosystem remains in a defined state (i.e., within some range of variability).
Resistance – The capacity of an ecosystem to adsorb or otherwise dissipate perturbations and prevent them from amplifying into large disturbances. Resistance mechanisms may be thought of as filters that reduce the potential for large disturbances or as those properties of systems and individuals that maintain relative constancy in processes and that prevent organisms from succumbing to some stress.
• **Resilience.**—The capacity of an ecosystem to return to the preperturbation state following a disturbance. Refers to the bounds in state space around which a system will vary but return to preperturbation state. If the system moves outside these bounds, it will move to another state. While the state to which the system recovers is unlikely to be an exact replica of what existed before, it nevertheless contains the same basic elements (species richness, habitats, soil fertility) and supports the same key processes (e.g., photosynthetic capacity and nutrient and hydrologic cycles). In other the words, system integrity is maintained.

• **Recovery.**—The speed with which an ecosystem returns to the preperturbation state following a disturbance.
It is worth noting that stability per se can be achieved in ecosystems in several different ways:

1. In systems that can be altered relatively easily (i.e., low resistance) but will return to the initial state rapidly (i.e., rapid recovery and high resilience). Such systems are often characterized by low biomass.

2. In systems that maintain a high resistance to disturbance and thus persist in a stable state for long periods of time. Such systems are often characterized by high biomass.

3. Physical system stability can be achieved in certain ecosystems. Such systems are characterized by the absence of biomass.
2. Landscape Equilibrium Concepts

Turner et al. (1993) reviewed several concepts of landscape equilibrium.

2.1. Absolute Constancy

The simplest concept of order that might be imposed on a landscape would be equilibrium in the sense of absolute constancy; that is, there are no changes through time. Clearly, however, disturbances and change are integral parts of landscape dynamics and make this notion of equilibrium unrealistic.
2.2. Shifting Mosaic Steady-State

In the shifting mosaic steady-state concept (Bormann and Liken 1979), the vegetation present at individual points on the landscape changes, but, if averaged over a sufficiently long time or large area, the proportion of the landscape in each seral stage is relatively constant, i.e., is in equilibrium (sensu Watt’s unit pattern). This concept emphasizes that even systems with a high disturbance frequency could be in a ‘steady-state’ or ‘equilibrium’ if the creation of new patches is balanced by the maturation of old ones (i.e., balance between disturbance and succession on a larger scale).
The shifting mosaic steady-state concept has been difficult to test empirically, but it has been suggested to apply to some systems.

- **Northern hardwood forests of New England**—predominant disturbance is windthrow of individual trees or small groups, resulting in a stable patchwork of gaps in various phases of succession (i.e., gap-phase succession), at the scale of a small watershed.

- **Balsam fir forests of the northeastern U.S.**—wave-regenerated forests, where natural ‘mortality waves’ move through the forest once every 50-70 years. Since the waves move at a fairly uniform rate, there are always freshly killed areas, and since consecutive waves are only about 100 m or so apart, an area of a few dozen hectares will normally contain all phases of the disturbance cycle.

These systems are said to be in equilibrium or quasi-equilibrium because disturbance is sufficiently frequent and small-scale compared to the landscape area that most populations and processes are fairly constant over the whole area.
The shifting mosaic steady-state concept is problematic as a general property of landscapes for several reasons.

- The concept is applicable only when disturbances are small and frequent in a large area of homogeneous habitat. Thus, large areas may be more likely than small areas to exhibit a stable mosaic. Few studies have identified stable mosaics even over relatively large areas.
• The concept assumes that the effects of discontinuities or gradients in topography, soils, moisture or other factors that would affect disturbance frequency or recovery are averaged across the landscape. This is a difficult condition to satisfy on real landscapes.
The concept is scale-dependent. Defining the sufficiently broad temporal and spatial scales over which to consider the aggregate mosaic is ambiguous. Equilibrium conditions do not exist at extremely fine and extremely coarse scales. It is conceivable to find a shifting steady-state mosaic on some landscapes at some intermediate scales, but it is difficult to specify the relevant spatial and temporal scale a priori.
2.3. Stationary Process

Another concept considers landscape equilibrium to be a stationary process with random perturbation. A stationary process is a stochastic process that does not change in distribution over time or space.

Loucks (1970) suggested that communities may appear unstable at any particular point in time because community composition is changing, but that the entire long-term sequence of changes constitutes a stable system because the same sequence recurs after every disturbance.

In fire-dominated landscapes, the statistical distribution of seral stages, fire return intervals, fire sizes, or similar parameters can be determined. This stationary process concept explicitly acknowledges the stochastic nature of disturbance, e.g., consider a probability density function for fire return intervals, but assumes that the distribution of fire return intervals (e.g., a negative exponential) remains more or less constant through time. Thus, the fire return interval may vary, and the probability of fire return may change with time since last disturbance, but when averaged over a sufficient large landscape and over a sufficiently long period of time, the statistical distribution remains relatively constant.
Unfortunately, the stationary process concept cannot escape the problems of scale discussed for the shifting mosaic steady-state concept. As with the steady-state, the stationary distribution cannot be achieved at extremely fine and extremely coarse scales, and it is difficult to specify the relevant spatial and temporal scale a priori.
2.4. Bounded Equilibrium

A concept related to the stationary process is that of stochastic or relative constancy through time. In this scenario, the system exhibits random changes (e.g., in response to stochastic disturbance events) but remains within bounds.

Unfortunately, the concept of a bounded equilibrium concept cannot escape the problems of scale. For example, long-term monotonic changes in climate due to global warming or glacial cycles would eventually move the landscape out of pre-set bounds. And not even reasonable bounds are sufficient to envelop a spatial extent larger than a biome.
Concepts of Landscape Equilibrium

- Bounded Equilibrium: Examples

Wimberly et al. (2000)
2.5. Homeorhetic Stability

With most concepts, equilibrium has been defined relative to some “undisturbed” state. A landscape has been considered as being in equilibrium if it remains in the neighborhood of some undisturbed state or remains balanced in the recovery stages leading to this undisturbed state. However, communities are in a constant dynamic process of adaptation to their environment such that stability in this sense may be unrealistic.

A more appropriate concept of stability may be that of ‘homeorhetic’ stability, which states that if perturbed, a system returns to its preperturbation trajectory or rate of change. Homeorhetic stability implies return to normal dynamics rather than return to an artificial “undisturbed” state.
3. Equilibrium or Nonequilibrium landscapes? – role of legacies, landscape uniqueness, and the importance of scale

Sprugel (1991) reviewed several examples of systems thought to be exemplary of the balance of nature in a "natural" state, including the African savanna, the "Big Woods" of Minnesota, lodgepole pine landscapes of the Yellowstone area, and old-growth forests in the Pacific Northwestern United States. He noted that in some areas an equilibrium may exist in which patchy disturbance is balanced by regrowth, but in others equilibrium may be impossible because (1) individual disturbances are too large or infrequent; (2) ephemeral events have long-lasting disruptive effects; and/or (3) climate changes interrupt any movement toward equilibrium that does occur.
Nonequilibrium Landscapes
Sprugel (1991)

- The African Savannas

- The Big Woods of Minnesota
Nonequilibrium Landscapes
Sprugel (1991)

- Lodgepole pine forest of Yellowstone

- Old-growth forest of the Pacific Northwest
Based on these and other examples, Sprugel concluded the following:

- "Natural" vegetation is far less stable than it may seem to be from our human perspective; in particular, most of the examples cited are nonequilibrium over time scales measured in life-times of the dominant organisms.

- Vegetation may preserve small or transient effects for a very long time, especially in the case of forests of long-lived trees.

- "Every point in time is special" in that, at any time, vegetation has some characteristics that distinguish it from the same system at any other time.

- Thus, it may be impossible (or irrelevant) to define the "natural state of the system" -- for many if not most systems.
Clearly, the concept of balance is unrealistic if balance is interpreted as “no change.” However, if we take balance to mean that some changes in the state of a system are consistent with maintaining species and processes, while other changes are not, then there clearly are balances in nature, and different kinds of disturbances can have quite different implications for the integrity of natural and managed systems.

While nature is dynamic, not all changes are consistent with maintaining system integrity. Numerous examples can be cited of changes in system state (e.g., species composition and processes) that are quite distinct from normal successional changes; in essence, sites convert to a new community that itself may be self-reinforcing. Perhaps the most widely known contemporary examples are the collapse of some forests due to excessive pollution and the worldwide desertification of arid grasslands, a phenomenon underlain by loss of soil integrity due to the combined effects of overgrazing and drought, exacerbated in many cases by an intensified disturbance regime due to the spread of flammable exotic grasses.
4. Disturbance and Landscape Equilibrium

Turner and colleagues used a simple simulator to address the question of how we might expect systems to behave over time, given a specific disturbance regime and a particular reference area (e.g., management district or study area) (Turner et al. 1993). They normalized the scaling of their system by defining the time scale as:

\[ T = \text{Disturbance Interval/Recovery Time} \]

and similarly, defined spatial scaling as:

\[ S = \text{Disturbance Magnitude/Landscape Extent} \]

which allows them to normalize systems of widely varying spatial dimensions or time scales.

They then simulated system dynamics as an interplay between a simple successional trajectory and system-resetting disturbances of various temporal and spatial scales. The next few slides summarize the major results of the simulation. Review the Turner et al. (1993) paper for the details of the study.
Disturbance and Landscape Equilibrium

Turner et al. (1993)

Fig. 2. Time series of the proportion (y) of the landscape occupied by (a) all 3 stages: 1, 4, 7, and 6, and (b) serial stages 1, 6, and 7 during a 100-time step simulation on a 100 x 100 landscape in which the temporal parameter \( T = 0.1 \) and the spatial parameter \( S = 0.5 \).

Fig. 3. State-space diagram of the temporal and spatial parameters used to describe potential disturbance dynamics which define (a) the region or in which the mature forest stage has a mean coverage > 90% of the landscape, (b) the region in which the pioneer forest stage has a mean coverage > 50% of the landscape, and (c) the region in which the intermediate forest stages have a mean coverage > 5% of the landscape.

Disturbance and Landscape Equilibrium

Turner et al. (1993)

Fig. 4. State-space diagram of the temporal and spatial parameters used to describe potential disturbance dynamics which define the regions of high and low standard deviation (SD) in the proportion of the landscape occupied by the mature forest stage during a simulation of 100 time steps.

Fig. 5. State-space diagram of the temporal and spatial parameters which illustrates regions that display qualitatively different landscape dynamics.
Fig. 6. State-space diagram of the temporal and spatial parameters which uses fire in Yellowstone National Park to illustrate effects of expanding the temporal scale of observations on conclusions regarding landscape dynamics.

Fig. 7. State-space diagram of the temporal and spatial parameters which uses treefall gaps in deciduous forests to illustrate effects of changing the spatial scale of observations on conclusions regarding landscape dynamics.
Briefly, Turner and colleagues concluded the following:

- Characteristic dynamics can be predicted from the relative scaling of the disturbance regime.
- Disturbance-driven landscapes might be equilibrium, quasi-equilibrium, or inherently nonequilibrium (or combo's of these).
- Anthropogenic influences may rescale these and change the qualitative dynamics of systems (e.g., fire suppression rescales a fire regime).
5. Anthropogenic Influences on Landscape Dynamics

Much of the interest in landscape dynamics is stimulated by the desire to understand how human activities have influenced landscapes, and how this understanding can inform land planning. Much of the focus has been on how anthropogenic changes in disturbance regimes have altered landscape patterns and dynamics. In particular, changes in fire disturbance regimes due to altered climate conditions or fire suppression activities, and the impacts of forest management activities, particularly logging, have received the most attention. Historical retrospective studies and spatial modeling have combined to provide important insights.

- Changing disturbance regimes can have an immediate effect on some measures of landscape pattern, no effect on others, and a significantly delayed effect on others. For example, Baker (1992) modeled the effect of human settlement and fire suppression on landscape structure in the Boundary Waters Canoe area in northern Minnesota. Settlement produced immediate effects on some metrics, including patch age, patch shape, and Shannon’s diversity, but no effect on others, including patch size and fractal dimension. Fire suppression resulted in immediate responses in a few metrics, but a delay of several decades in patch age and fractal dimension and a delay for hundreds of years in others (patch size). Thus, the effects of changes in disturbance regime may not be observed for many years, making it difficult to document the impacts.
Altered disturbance regimes can have a long-lasting ‘legacy’ effect on landscape dynamics; that is, human-altered disturbance regimes can have an impact on landscape pattern dynamics that may persist long after the disturbance regime has returned to ‘normal’. For example, Wallin et al. (1994) modeled changes in landscape structure in response to alternative anthropogenic (forest cutting) disturbance regimes. This study was motivated by the question of how long a pattern imposed by a particular forest cutting pattern would persist once the disturbance regime was changed, for example, if forest harvest was to cease or if return intervals were to be lengthened considerably.
Their results demonstrated that the landscape pattern created by dispersed disturbances was
difficult to erase without a substantial reduction in disturbance rate or reduction in the
minimum stand age eligible for disturbance. Even after only 20 yr of dispersed cutting, the
switch to aggregated cutting produced only small changes in landscape patterns as reflected
by edge density and mean size of interior forest patches; after 40 or 60 years of dispersed
cutting, the change in disturbance regime produced an even smaller effect. This study
demonstrated that the response of landscape pattern can lag substantially behind a change in
the disturbance regime.
In the same study, Wallin et al. (1994) also demonstrated a more general impact of alternative forest cutting scenarios on the dynamics in landscape structure. Specifically, they conducted a historical reconstruction of vegetative cover classes dating back to 1560 in two watersheds in the westside Cascade Mountains in Oregon. In addition, they simulated several alternative, but realistic, forest cutting scenarios under debate at the time by forest managers and policymakers. In addition to the rather obvious result that more intensive cutting regimes resulted in less mature, closed-canopy forest being sustained on the landscape over time, they also demonstrated the potential for all cutting scenarios to dramatically alter the dynamic behavior of the landscape. Specifically, under all cutting scenarios, which involved complete regulation of the forest, the variability in landscape structure over time was severely dampened or eliminated compared to the historic range of variability (as defined), thus dramatically altering the landscape dynamics. While several scenarios maintained the landscape structure within its historic range of variability, the ecological impacts of removing the dynamic behavior of the landscape was less clear.
Anthropogenic Influences
Wallin et al. (1994)

(a) Landscape Patterns in 2190 - Lookout Creek

- 50 yr-agg
- 100 yr-disp
- 200 yr-agg
- 330 yr-agg
- 100-330 yr-agg

Legend:
- Red: Open-canopy forest (< 40 yrs)
- Black: Closed-canopy forest (> 40 yrs)

Anthropogenic Influences
Wallin et al. (1994)

(a) % Landscape in Closed-canopy Forest

Lookout Creek

Year
6. Management Implications

Understanding the dynamics of a landscape has numerous management implications. Here, we will consider just a few.

- While managing for a stationary pattern may seem appealing from a purely pragmatic standpoint, the simple fact is that in most real landscapes a stationary pattern is unlikely to be attained, and certainly cannot be sustained over time. Knowing the natural range of variability for a system can put bounds on expected dynamics -- so we can temper our expectations and react appropriately to realistic variability. This knowledge would also provide a reference against which to compare the system, i.e., to identify when the system seems to be going "out of normal bounds" and some management intervention seems justified. One of the greatest practical difficulties in quantifying landscape structure and interpreting landscape patterns is the lack of a good context or reference condition. Providing a quantitative understanding of the range of natural variation in landscape structure metrics will allow managers to better interpret the current landscape structure and alternative future landscape structures.
Management Implications  
*(Roworth et al. Unpubl Report)*

**Base Scenario**  
*Percent Landscape Late Seral Forest*

- First 2 principal components accounted for roughly 80% of the variation in late seral forest amount and configuration.
- Fragmentation gradient accounted for 52-62% of the variance; interspersion accounted for an additional 16-19%.
Management Implications
(Roworth et al. Unpubl Report)

Fragmentation (68%)

Interspersion / Contrast (17%)

Management Implications
(Roworth et al. Unpubl Report)

Fragmentation (68%)

Interspersion / Contrast (17%)
Not only are ecosystems and landscapes dependent on natural disturbances, but many ecological processes and organisms appear to be dependent on the actual “dynamics” associated with changes in the system. Understanding the nature of these dependencies is one of the greatest challenges facing landscape ecologists. If for example, the periodic or episodic changes in the state of the landscape (e.g., caused by large-scale disturbance) is essential for the maintenance of biodiversity, then management strategies will need to embrace such dramatic changes in the state of the landscape instead of trying to dampen the fluctuations in state caused by disturbances.
Management Implications
(Reeves et al. 1995)
Management Implications
(Reeves et al. 1995)

Hypothetical historical conditions of fish habitat in different streams within and among watersheds

Management Implications
(Reeves et al. 1995)

Patterns resulting from (A) dispersing and (B) concentrating land forest cutting activities in a watershed over time.
Management Implications
(Reeves et al. 1995)

Patterns resulting from (A) dispersing and (B) concentrating land forest cutting activities in a watershed over time

(A) Dispersed Cutting

(B) Concentrated Cutting

Management Implications
(Reeves et al. 1995)

Patterns of variability resulting from (A) anthropogenic and (B) natural disturbances in relation to spatial scale

Ecosystem structure & function (state variable)

Time

Anthropogenic Regime

Natural Regime
Land management strategies are often established to ensure that viable populations of all species are maintained over space and time. This is often interpreted to mean maintaining steady or increasing populations of all species. Consequently, population declines are almost always viewed as cause for concern. Better understanding the natural dynamics of wildlife populations will allow managers to distinguish between natural population fluctuations associated with the natural dynamics of the landscape and human-induced fluctuations that force a population outside the range of natural variability.
Management Implications
(Crist et al. Unpubl. Report)

- American Marten
  - Olive-sided Flycatcher
  - Three-toed Woodpecker
  - Elk

Management Implications
(Crist et al. Unpubl. Report)

- Local
  - Composition = f(vegetation type, seral stage, disturbance history)
  - Context = f(juxtaposition, edge effects, topography)

- Landscape
  - Composition = f(extent of high quality habitat within home range area)
  - Configuration = f(fragmentation of high quality habitat within home range area)
Management Implications
(Crist et al. Unpubl. Report)

Three-toed Woodpecker

American Marten

Management Implications
(Crist et al. Unpubl. Report)

Elk

Olive-sided Flycatcher
Management Implications
(Crist et al. Unpubl. Report)

- Amount
  - Percent of landscape in suitable habitat

- Configuration
  - Contagion Index
  - Correlation length
  - Proximity Index
  - Similarity Index

Management Implications
(Crist et al. Unpubl. Report)
Management Implications
(Crist et al. Unpubl. Report)

Contagion

Pland

Management Implications
(Crist et al. Unpubl. Report)

Stable high quality habitat