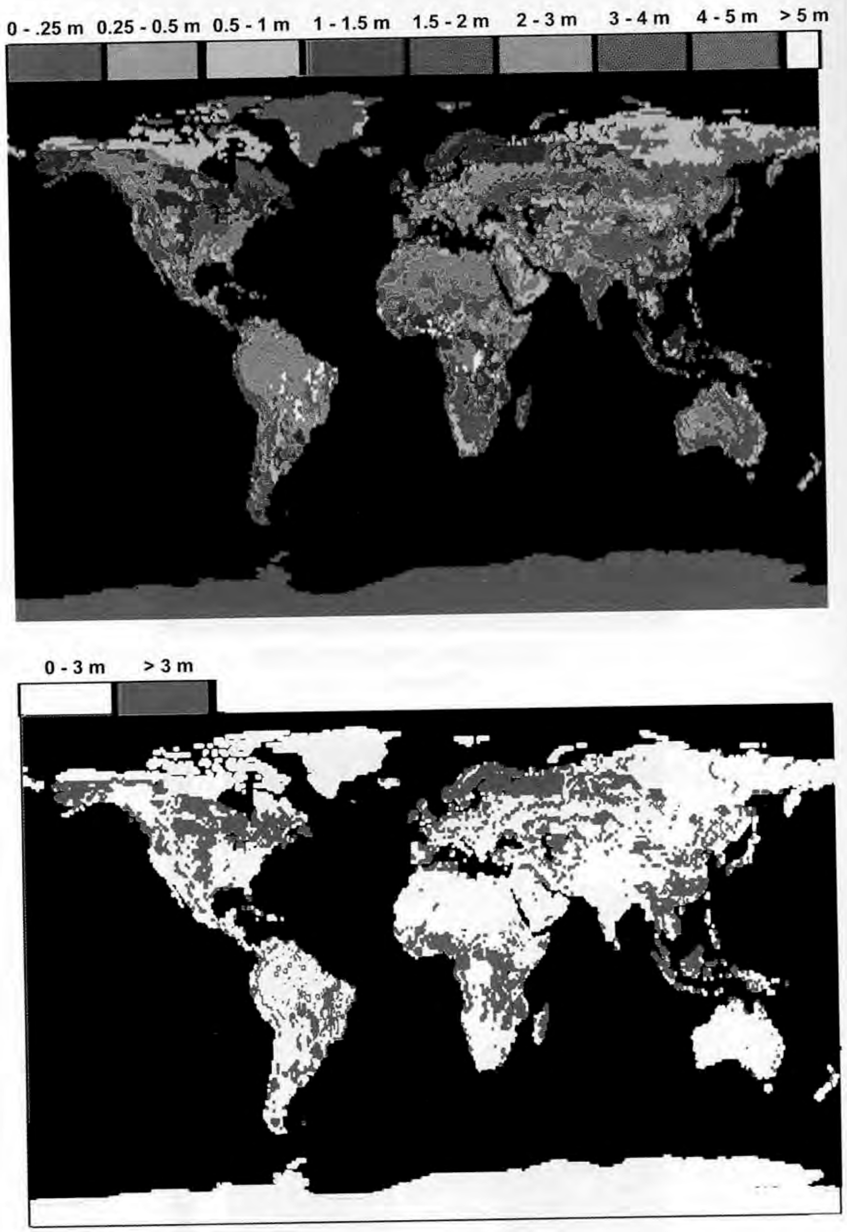

Plate 11.1

14

Do Landscape Structural and Functional Units Exist?

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ABSTRACT

The complexity of landscapes requires that we develop simplified constructs or frameworks for understanding and predictions. Toward this goal, we pose the question, "Do landscape structural and functional units exist?" We argue in favor of the existence of landscape units, but acknowledge that there are no generic recipes for simplifying the real world for use in landscape models. While simplification is the key to achieving understanding and prediction, explicit consideration of scale multiplicity in studying complex landscapes is dictated by the hierarchical properties of landscapes. Therefore, we suggest that the hierarchical patch dynamics paradigm provides a conceptual framework to accomplish these objectives.

INTRODUCTION

At coarse scales, landscapes are usually envisioned as mosaics of various landforms, biological communities, and land uses. Such human-perceived landscapes (tens to hundreds of kilometers wide in area) tend to dominate our view of landscapes because of their relevance to pressing questions in conservation ecology, resource management, and environmental planning (Forman 1995; Pickett and Cadenasso 1995). Research at the scale of landscapes is a recent emphasis in ecology. The traditional approach has been more of a "vertical" perspective, where a system is viewed as spatially homogeneous and, hence, the internal processes and function are highlighted; in contrast, the landscape approach is more of a "horizontal" perspective since it focuses on the spatial distribution of — and interactions among — ecological entities (Rowe 1961). The vertical perspective promotes a process- or function-based approach (e.g., ecophysiology, population and ecosystem dynamics), whereas the horizontal perspective tends to encourage a structural, pattern-oriented, or geographic approach (e.g.,

Integrating Hydrology, Ecosystem Dynamics, and Biogeochemistry in Complex Landscapes
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studies of spatial patterns of individuals, populations, and communities at relatively fine scales and biogeography at coarser scales).

The theme of this multidisciplinary Dahlem workshop was to integrate understanding of *both* the vertical and horizontal perspectives of hydrologic, ecosystem, and biogeochemical processes in landscapes — including important feedbacks, disequilibria, and inertia. This is an enormous challenge. Perhaps the greatest challenge is to design appropriate experiments and to build models that will permit us to extrapolate results from our traditional short-term and small-scale empirical studies to the larger temporal and spatial scales of landscapes. The complexity of landscapes requires that we develop simplified constructs or frameworks representing the real world.

Toward this goal, we pose the question, "Do landscape structural and functional units exist?" Presumably, an affirmative answer to this question implies that generic recipes are available for simplifying the real world for use in landscape models. While we argue that landscape structural and functional units *do* exist, such recipes *do not,* in that each case study is dependent on its specific objectives and the relevant spatial and temporal scales. There are, nevertheless, some useful tools that can greatly aid us in modeling landscape dynamics. In this chapter, we describe hierarchy theory and the hierarchical patch dynamics paradigm in this context. Our general question, "Do landscape structural and functional units exist?" leads to more detailed questions, for example: Do landscapes function as assemblages of "patches?" What criteria and methods may be used to delimit the scale at which ecosystem processes may be considered homogeneous? What determines the size or structure of landscape "patches"? Can hierarchical scaling help simplify landscape complexity? Can we determine if one landscape is "more" heterogeneous than another? Is it possible to develop landscape models based on current knowledge, which is usually not at the landscape level but at much smaller spatial and temporal scales?

LANDSCAPE STRUCTURE: HETEROGENEITY AND PATCHINESS

In a broad sense, a landscape may simply be defined as a geographic area in which ecological processes of interest are significantly affected by spatial pattern. This definition has several important implications that frame much of what we present in this chapter:

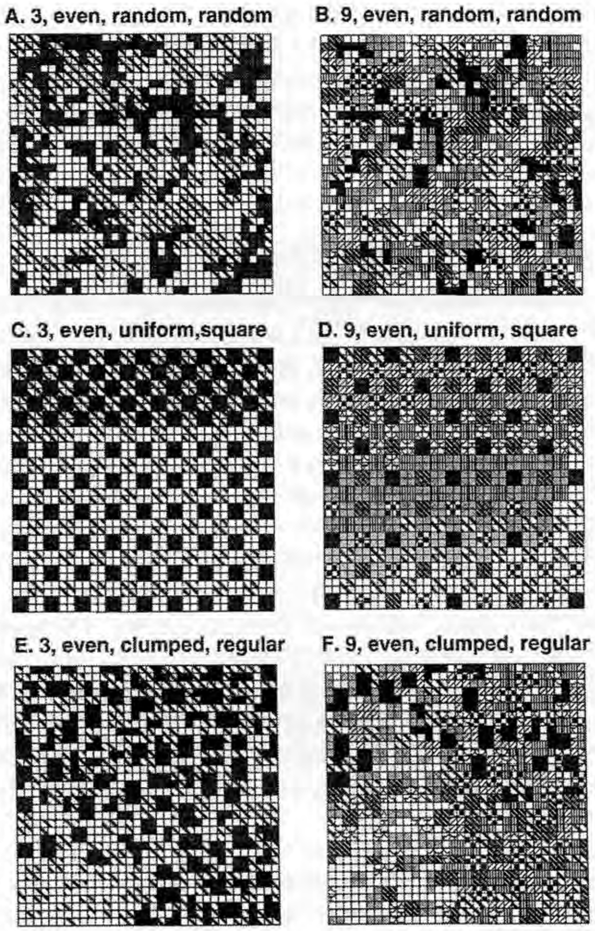
1. A landscape may be understood as an ecological criterion rather than a geographic area with a fixed spatial scale (Pickett and Cadenasso 1995).
2. The spatial scale of a landscape is dependent upon specific ecological processes or organisms under study (Kotliar and Wiens 1990).
3. Considering that spatial pattern and ecological processes operate over a range of different scales within a geographical area, the multiplicity of scale is inherent in the study of landscape ecology (Wiens 1989).

In this section, we introduce three topics crucial to the concept of landscape structural units. First, we introduce the notion of the patch as the basic element of landscapes; second, we define spatial heterogeneity in terms of what it is (and is not) and describe some of the issues and problems of quantification; and third, we describe Cantwell and Forman's (1993) scheme for reducing inherently complex landscapes to a common structure.

Patch: The Basic Element of Landscape Structure

Six computer-generated landscape maps are shown in Figure 14.1. The scale of these maps is arbitrary and for our purposes here, we assume that each represents an area of 32 km × 32 km, where each 1 km^2 cell in the grid is one of nine different *patch* types (black, white, grey, left-hatched, right-hatched, etc.). The eye immediately discerns different patterns for each map, which are not unlike some of the landscape mosaics we might see when flying across Europe in an airplane. Such patterns are the hallmark of a landscape (Urban et al. 1987). Hence, we could also define a landscape as a geographic area composed of "patches," which in the real world are such entities as forest types, farmland, residential areas, lakes, etc. When high up in the air, coarse-grained patches composed of large tracts of forests, croplands, and lakes are evident as well as some characteristics of their spatial configuration (e.g., adjacency of different patch types, shapes). When taking a bird's-eye view of these same landscapes, one may see not only the patches themselves but also their spatial pattern change as a function of the distance to the ground. Nearer the ground, as we are landing at the airport (say, *within* a km^2), the obvious patches we see are localized forest remnants, residential areas, city parks, and golf courses, and their spatial pattern may differ significantly from that we saw at coarser scales.

Patchiness exists at all spatial scales so what we define as a patch is dependent on our scale of interest and measurement system (Kotliar and Wiens 1990). For both modeling and experimental purposes, we usually consider patches to be relatively discrete and internally homogeneous units that are quantitatively and qualitatively different from their immediate surroundings. For example, imagine that map A in Figure 14.1 represents a satellite image of 1,064 hectares of a desert landscape in southern New Mexico, where the black patches represent grass communities, the cross-hatches are shrub communities, and the white patches are sand dunes. We see that some of each of the three patch types are adjacent to one another and thus form larger (1 ha) patches of irregular shapes. At a different scale, these three patch types — which show up in the satellite image as relatively homogeneous — are, in fact, not. To illustrate this, imagine that map E represents *one* of the 1 ha black (or grass) patches in map A. Map E is itself composed of three distinct patch types: black represents grass cover, cross-hatches are herbaceous plants, and white is bare soil. Each patch type in map E is ≈10 m^2 but again, adjacent patches of similar types form larger patch sizes of each type. Logically, we could continue to go down in spatial scale, eventually to the level of a single grass



A. 3, even, random, random
B. 9, even, random, random
C. 3, even, uniform,square
D. 9, even, uniform, square
E. 3, even, clumped, regular
F. 9, even, clumped, regular

Figure 14.1 Simulated landscape maps. Levels of four map-generating components of spatial heterogeneity are indicated on the top of each map: i.e., the number of patch types (3 or 9), proportions of each patch type (even, uneven), the spatial arrangement of patches (random, uniform, clumped), and patch shape (square, regular, random). These maps show comparisons between two levels of the number of patch types, three levels of the spatial arrangement, and three levels of the patch shape. Mean patch size is four for all maps. From Li and Reynolds (1994).

clump, which itself is heterogeneous in terms of leaf nitrogen distribution, stomatal density, etc.

What causes patchiness? A wide number of both natural and anthropogenic agents play a role in creating and maintaining patchiness, including natural and human disturbances (e.g., fire, erosion, tree windfalls, clear-cutting, farming, pest outbreaks, development), land management, soil and landform factors, and biological interactions (e.g., competition, predation) (see Forman and Godron 1986; Holling 1992; Turner 1989; Wu and Loucks 1995). For convenience, we can view spatial patchiness from either abiotic or biological perspectives, both of which operate interactively across a range of spatial, temporal, and organizational scales. At continental or global scales, climatic variables — primarily temperature and precipitation — are largely responsible for the spatial pattern in vegetation. From the local ecosystem (e.g., a stand of trees) to landscape scales, patchiness is usually a result of factors such as disturbance, aspect (i.e., north- vs. south-facing slopes of a mountain), and geomorphology (e.g., floodplain of a river). Biological interactions such as competition, predation, and complex plant–soil processes can affect patchiness at finer scales.

Spatial Heterogeneity: What Is It and How to Measure It?

Are quantitative indices available to represent landscape structure? Is the patchiness evident in Figure 14.1 equivalent to landscape structure? This brings us to the concept of spatial heterogeneity.[1] While spatial heterogeneity is perhaps the single most important concept in landscape ecology, it has many different meanings and usage in the literature (Dutilleul and Legendre 1993; Kolasa and Rollo 1991; Li and Reynolds 1995; Wu and Loucks 1995). Towards resolving some of this confusion, Li and Reynolds (1994, 1995) proposed various guidelines, which we briefly summarize here. They define spatial heterogeneity as the *complexity* and/or *variability* of a system property in space and/or time. A system property is anything of interest that we wish to measure in the landscape, e.g., normalized difference vegetation index (NDVI), soil nutrients, vegetation cover, topography, and this system property can be measured either by its complexity (that is, qualitative or categorical descriptors) or its variability (quantitative or numerical descriptors) (see Figure 14.2). This is important because it says that landscapes have characteristics that can be observed and measured. Of interest to us are *structural heterogeneity*, that is, the complexity or variability of a structural property (vegetation cover, soil nutrients, elevation, etc.) and *functional heterogeneity*, that is, the complexity or variability of a functional property (gas flux, primary productivity, etc.).

As illustrated in the example of maps A and E, whatever heterogeneity we attempt to measure will be a function of the scale we choose. This can best be understood in terms of grain and extent, two of the primary scaling factors that affect complexity and

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[1] "Spatial heterogeneity" and "patchiness" are used somewhat interchangeably in the literature. Jarvis (1995) defines patchiness as "organized heterogeneity of a number of properties," e.g., the patchiness of a landscape composed of a forest plantation, a wheat field, and a pasture results from the fact that these vegetation types are "organized" into discernible patches; if the individual plants of each vegetation type were randomly mixed and distributed over the same landscape (i.e., "unorganized"), patches would not be evident. Our consideration of spatial heterogeneity in this section gives a more explicit meaning to patchiness.

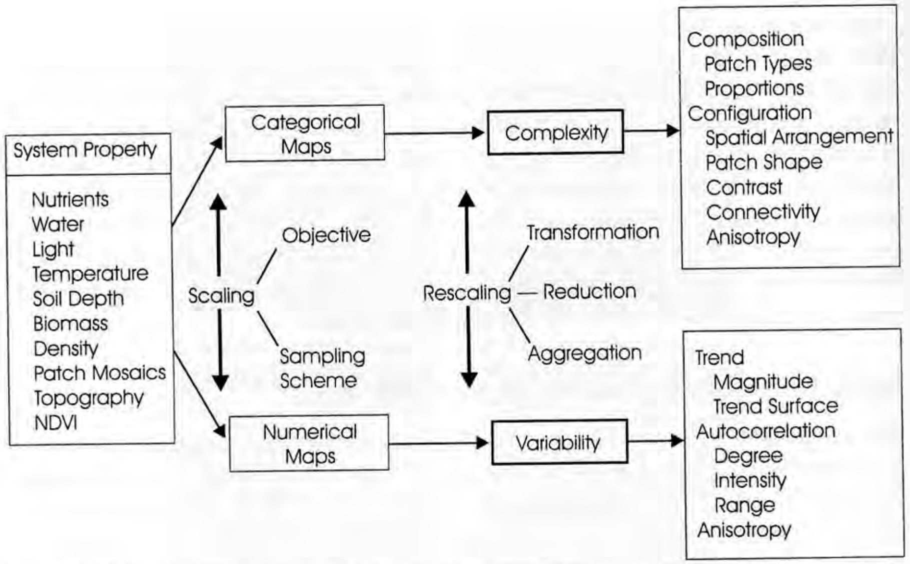

Figure 14.2 Overview of scheme for quantifying spatial heterogeneity. From Li and Reynolds (1995).

variability and, hence, heterogeneity. *Grain* is the finest resolution of data (e.g., the pixel size in Figure 14.1, minimum time step for time series data) and *extent* is the area or duration encompassed by a study. So, in any landscape study, we choose an observational scale (i.e., grain or extent) and a sampling scheme based on our research objective and the nature of the phenomenon of interest and these resultant data determine what kind of heterogeneity can be measured. It must also be emphasized that, from a data analysis viewpoint, *rescaling* of data — including transformations, data reduction and aggregation, and resampling — is also a form of scaling. Rescaling may modify grain or extent or both and, hence, plays a role in how we actually quantify heterogeneity (Figure 14.2).

Which of the six landscapes in Figure 14.1 is the "most" heterogeneous? This is a critical issue since we are interested in how landscape structure (pattern) affects (and is affected by) hydrologic, ecosystem, and biogeochemical processes. However, quantifying heterogeneity is far from a straightforward exercise. Although a large number of indices have been developed that quantify spatial heterogeneity (see Kolasa and Rollo 1991; Turner et al. 1991), what they actually are measuring is somewhat equivocal. We illustrate this with an example. As shown in Figure 14.2, landscape maps may be either categorical or numerical, depending on the data types used — and this determines what type of index or method is appropriate (Table 14.1). In the case of Figure 14.1, which contains six categorical maps, spatial heterogeneity (SH) is measured by its complexity in *composition* and *configuration* of the patches. Composition includes the number of different patch types (NPT) and the proportions of each type (PET), while configuration includes spatial arrangement of patches (SA), patch shape (PS), contrast between neighboring patches (NC), connectivity among patches of the same type, and anisotropy (i.e., variation in different directions). The maps in Figure 14.1 were generated by the SHAPC simulation model that controls five of these components of complexity, that is:

$$SH = f\{NPT, PET, SA, PS, NC, \varepsilon\} \tag{14.1}$$

where ε is the random error (for details, see Li and Reynolds 1994). To generate a particular landscape map, each of these components is set to a specific level (see legend in Figure 14.1). Using SHAPC, Li and Reynolds (1994) examined the relative contributions or influence of NPT, PET, SA, PS, and NC on different landscape indices and concluded that any definition of SH is strongly dependent on the underlying variables and the methods used, i.e., different indices depict different aspects of SH, significant interactions exist among the various components of SH, and some indices are strongly correlated.

Table 14.1 Examples of data types and methods for quantifying heterogeneity. From Li and Reynolds (1995).

Data Type	Description	Indices
Point pattern	Variables or individuals of species distributed at discrete locations	• Parameter *k* of negative binomial • Nearest neighbor index • Block-size variance statistic
Geostatistical	Continuous variables sampled regularly or irregularly in space	• Variogram • Correlogram • Fractal dimension
Quantitative lattice	Numerical maps	• Variogram • Correlogram • Autocorrelation indices
Qualitative lattice	Categorical maps	• Diversity indices • Fractal dimension • Patchiness index • Contagion index • Joint-count statistic

Can we say one landscape is "more" heterogeneous than another? Two categorical maps representing mosaics of cover types are shown in Figure 14.3. These "landscapes" were created with SHAPC (PET, SA, and PS were varied in Eq. 14.1; see Table 14.2) and four spatial indices (evenness, fractal dimension, contagion, patchiness) were used to quantify their heterogeneity. Map A has higher values of evenness and fractal dimension, while map B has higher values in contagion and patchiness (Table 14.2). From this we may conclude that "landscape" A is more diverse and contains

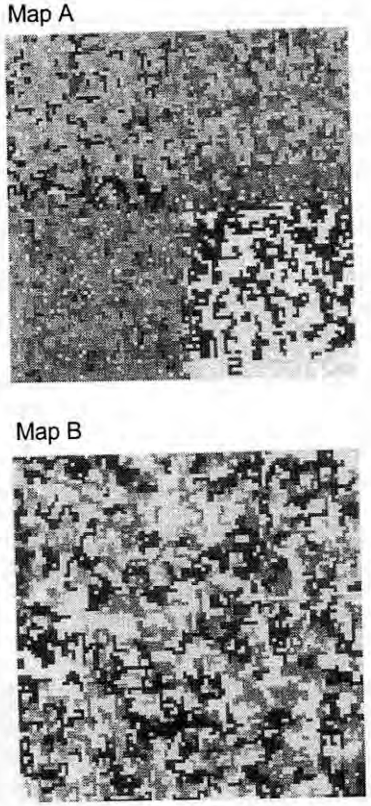

Figure 14.3 Two categorical maps generated from simulation parameters in Table 14.2. From Li and Reynolds (1995).

more irregularly shaped patches, whereas "landscape" B has larger patches and higher contrast. So, instead of asking the question of which landscape is "more" heterogeneous, it makes more sense to ask how two landscapes might differ with regard to some *specific aspect* of spatial heterogeneity of interest. For example, the various schemes used in clear-cutting forests differentially affect NPT, PET, SA, PS, and NC and, hence, will affect ecosystem dynamics in different ways. Bierregaard et al. (cited in Pickett and Cadenasso 1995) found that the number of carrion beetles and bird diversity in Amazon forests declines with the size of residual forest fragments, whereas Franklin and Forman (1987) showed that the degree of systematic "checkerboarding" remaining after clear-cutting in the U.S. Pacific Northwest was the main determinant of the susceptibility of old growth forests to catastrophic windthrow. Each component of heterogeneity (Equation 14.1) characterizes or represents a distinct aspect of spatial heterogeneity and thus it is important to define explicitly which component is of interest. More detailed treatments of this subject are given in Turner (1989), Dutilleul and Legendre (1993), Kolasa and Rollo (1991), Pickett and Cadenasso (1995), and Li and Reynolds (1994, 1995).

Table 14.2 Simulation parameters used in Equation 14.1 and the heterogeneity measures for the categorical maps shown in Figure 14.3. From Li and Reynolds (1995).

	Map A	Map B
Map Characteristics (simulation, see Eq. 14.1)		
No. of patch types (NPT)	6	6
Proportion (PET)	Even	Uneven
Spatial arrangement (SA)	Aggregated	Random
Patch shape (PS)	Random	Regular
Heterogeneity Measures		
Evenness	1.000	0.819
Contagion	0.152	0.196
Fractal dimension	1.640	1.603
Patchiness	0.296	0.550

Landscape Graphs: Common Structure

Cantwell and Forman (1993) introduced the concept of landscape graphs for reducing complexity in landscapes to a common structure. Landscape graphs define common structural units that may correspond to distinctive functional characteristics. While graphs may well differ with the scale of observation, it is interesting and useful to investigate if there are common landscape graphs across scales. This method is described and illustrated in Figure 14.4. Cantwell and Forman's goals were (a) to identify common structural configurations within landscapes; (b) to examine the connectivity of patches; and (c) to identify potential links to various landscape modeling approaches. The strength of Cantwell and Forman's scheme is their emphasis on *structural links between adjacent patches*, which are where functional exchanges of mass and energy may occur and thus are important in models of landscape functional units (see below).

Using the method of Figure 14.4, Cantwell and Forman developed graphs of 25 aerial photographs that represented a range of human-dominated landscapes. The predominant patch types represented in these photographs included forestry, pastureland, cultivation, suburbia, and "natural" vegetation, e.g., a pastureland in southern Wisconsin, a tropical rainforest with shifting cultivation in the Dominican Republic, several agriculture fields in Australia, suburban Chicago, and string bogs and a spruce forest site in Canada. They found seven distinctive patterns of nodes and linkages (i.e., they were present in > 3 graphs) (Figure 14.5). Of the seven patterns, three (necklace, spider, and loop) were found in > 90% of their graphs.

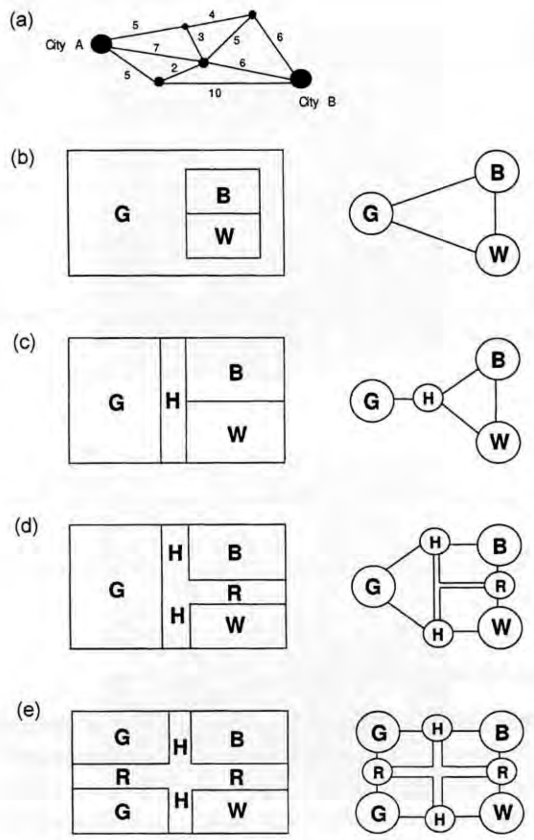

Figure 14.4 Landscape graphing methods. Landscape patch types are: G-grassland; B-bean field; W-woods; H-highway; and R-road. (a) Transportation graph with spatially-explicit linkage lengths representing distances between cities; size of the node size indicates relative city size. (b)–(c) Landscape areas and their corresponding graphs; nodes (circles) represent patch types (ecosystems, land uses) in the landscape, and linkages (lines) represent shared boundaries or points between patches. (b) Landscape graph of a matrix and two patches, recognizing the matrix as an element. (c) Landscape graph recognizing a corridor (highway) as an element. (d) and (e) Landscape graphs where a corridor network is represented as comprised of component elements, or lengths of corridor defined by intersections. (d) Landscape graph recognizing a 3-way or T-intersection, (e) Landscape graph recognizing a 4-way or X-intersection, and where one corridor axis predominates over the second. Redrawn from Cantwell and Forman (1993).

We refer the reader to Cantwell and Forman (1993) for details of the ecological interpretation and significance of these structural landscape patterns. Here we limit our discussion to a single one — the necklace — to illustrate the ecological consequences. The necklace patterns in Cantwell and Forman's human-dominated landscapes are all composed of the same landscape element (or patch) type linked together in a linear fashion, e.g., roads, hedgerows, or powerline corridors. They also found

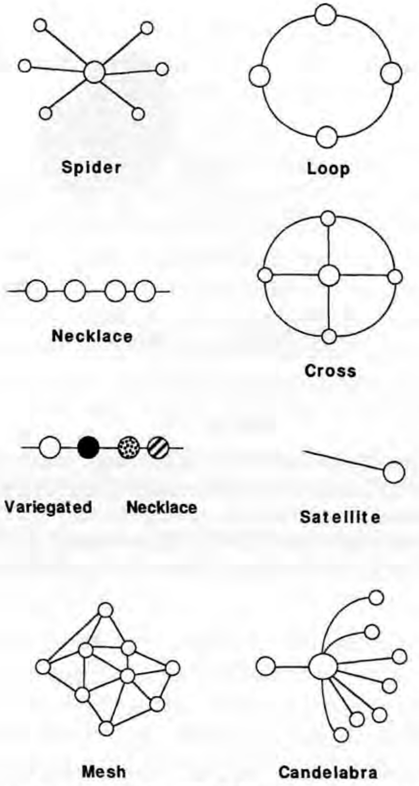

Figure 14.5 Common graph patterns identified from 25 diverse landscapes using approach described in Figure 14.4. Modified and redrawn from Cantwell and Forman (1993).

"variegated necklace" patterns where the elements are different, which is similar to what Woodmansee (1990) labeled a "flow path." In the case of coarse-scale landscapes, distinct geomorphic surfaces (e.g., alluvial fans, piedmonts) or topographic features (e.g., watersheds) often form natural boundaries for necklaces or flow paths. Several examples illustrate this principle. Kemp et al. (1997) described a toposequence established on a gently sloping, NE facing piedmont of a small mountain characteristic of the basin and range topography found in the southwestern U.S. This toposequence extends for 2.7 km from a basin floor playa (1310 m elevation, fine-textured soil), across a piedmont slope, and onto the base of a granitic mountain (1410 m elevation, coarse-textured soil). The gradients in elevation and soils across the transect, along with variable seasonal rainfall, downslope redistribution of water and organic matter, and soil texture-related variation in infiltration, water holding capacity, and moisture release characteristics, interact to generate a complex spatial and temporal gradient of patch types, available soil water, and nitrogen along the toposequence. In the mulga woodlands of eastern Australia. Ludwig et al. (1994) described a series of toposequences that are dotted with groves of mulga (*Acacia*) trees that act as "filters,"

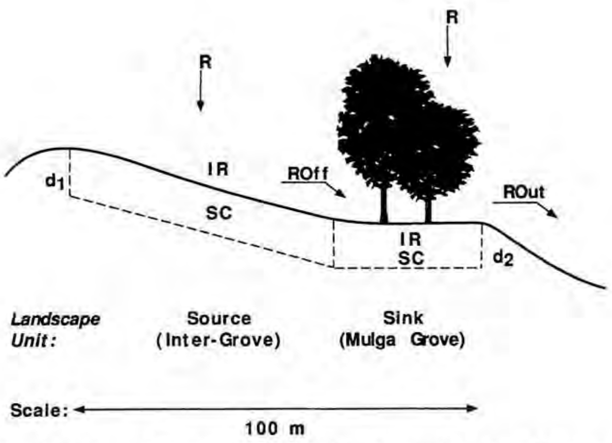

Figure 14.6 Vertical view of idealized semi-arid landscape in eastern Australia, depicting the flow of water by run-off (ROff) following rainfall events (R) when the amount and intensity of R exceeds the infiltration rate (IR) or the water storage capacity (SC) of the soil. The soils are deeper in depth within landscape sinks (d2) than under slopes (d1). Water not captured by the lowest sink runs out (ROut) of the landscape system. Redrawn from Ludwig et al. (1994).

capturing water (and nutrients, etc.) from barren inter-grove areas (see Figure 14.6). They described most of the semi-arid woodland landscapes in eastern Australia as composed of such complex toposequences, with repeating grove-intergrove units. In a small Alaskan watershed, Walker and Walker (1996) identified five patch types — crest, shoulder, upper backslope, lower backslope, and footslope — that form a necklace pattern; these patches are distinguished on the basis of differences in soils, vegetation physiognomy, geologic surface forms, and plant community types.

RELATING LANDSCAPE FUNCTION TO STRUCTURE: A HIERARCHICAL APPROACH

Given the ubiquitous existence of patchiness in ecosystems, is there a relationship between landscape structure and function? Not surprisingly, empirical evidence supports a strong, reciprocal relationship between patchiness (and the various components that comprise spatial heterogeneity) and ecological function or process. This relationship exists across a wide range of ecosystems and different types of functions, e.g., animal behavior, biogeochemical cycling, primary productivity (see Pickett and White 1985; Swanson et al. 1988; Turner 1989; Turner et al. 1995). However, while a great number of empirical and theoretical studies favor a strong link between landscape structure and function — and this is the central focus of much current research in landscape ecology (Pickett and Cadenasso 1995; Turner et al. 1995; Wu and Loucks 1995) — there are no "hard rules" available to guide our efforts in modeling complex landscapes. Instead, there are some general schemes or approaches that have emerged that, along with various modeling approaches, provide us with strong conceptual and analytical tools to address landscape functioning. In this section, we discuss how landscape structure affects function and how the hierarchical nature of this structure is a powerful tool that can be used to model function.

In the previous section we suggest that identifying *landscape structural units* involves a "synthesis" approach in which variations in patchiness are integrated over the entire landscape into a synoptic index to reflect the degree of landscape complexity or variability. In this section we argue that identifying *landscape functional units* requires more of an "analysis" approach, whereby landscape heterogeneity is partitioned hierarchically so that relatively homogeneous functional units can be distinguished. Conceivably, the same mathematical and statistical methods used to quantify landscape structural units can also be used to identify functional units when applied in a hierarchical manner.

Hierarchical Properties of Landscapes

From our discussion of patches and spatial heterogeneity, it is obvious that the structure of landscapes is hierarchical in nature (see reviews in Holling 1992; Urban et al. 1987; Wickham and Norton 1994; Woodmansee 1990). This is nicely illustrated in our example of maps E and A in Figure 14.1. Map E has unique structure at one scale (1 ha) that is not evident when viewed as a pixel in map A (which in turn has its own unique patchiness). Woodcock and Harward (1992) presented a schematic representation of forested landscapes as a nested hierarchy (Figure 14.7). Their objects or patches at the lowest scale in the hierarchy are individual trees, which may be of different sizes and species. The next scale of objects correspond to forest stands that are characterized by the collective attributes of the individual trees, e.g., the relative amount of conifers vs. hardwoods, overall density of trees, and aerial extent. A collection of stands form forest type objects, which in turn, form vegetation types. In a similar way, Reynolds et al. (1997) used a hierarchical approach to model desert landscapes (Figure 14.8). A patch at the lowest scale in their hierarchy is the average size of a single type of plant (grass clump or shrub) growing on a particular soil type (e.g., sandy-loam soil). Two general types of vegetation patches are recognized: grass and shrub islands, the latter of which is composed of a single shrub, representing a "hot spot" or "island" of biological activity within a matrix of relatively barren soil. Contiguous patches form patch mosaics where the strength of individual interactions is in part determined by spatial proximity (see Aber et al., this volume). In this system, they view landscapes as consisting of several patch mosaics (Figure 14.8).

Previously, we defined functional heterogeneity as the complexity or variability of a functional property, e.g., gas flux or primary productivity (see Figure 14.2). Thus, nested structural hierarchies are useful ways to "organize" and model landscape function. This approach builds on both the "vertical" and "horizontal" perspectives of viewing ecosystems and landscapes (see **INTRODUCTION**) where, at each level in the hierarchy, emphasis is placed on internal structure and function (vertical) whereas the

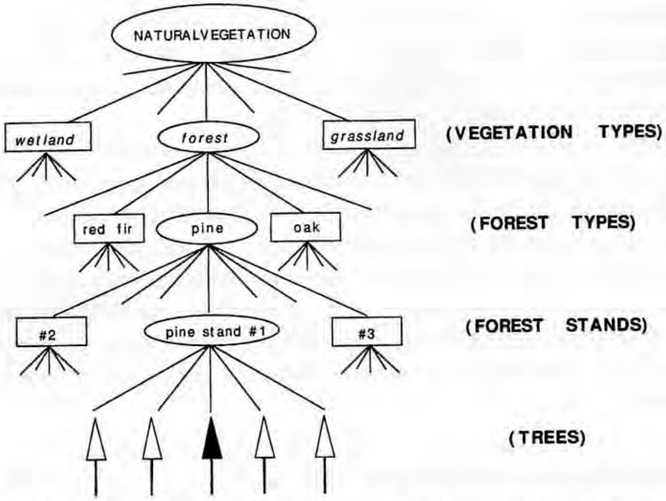

Figure 14.7 Schematic representation of forested landscapes as a nested hierarchy. Redrawn from Woodcock and Harward (1992).

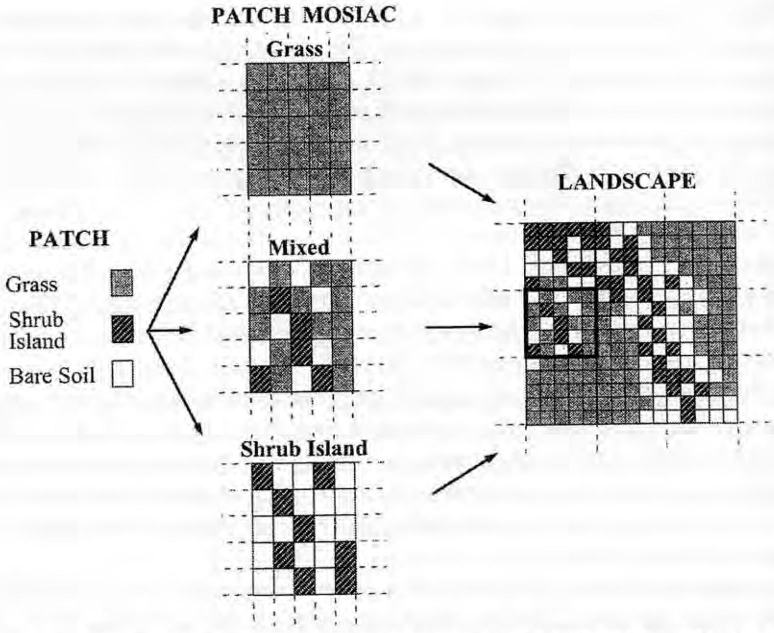

Figure 14.8 Landscape hierarchy for an arid ecosystem in southern New Mexico. Patches (ca. 1–10 m^2) form patch mosaics (ca. 1 ha – 1 km^2), the behavior of which is a function of its composition (number and proportion of different types of patches) and configuration (e.g., spatial distribution, shapes, contrast, etc.). Landscapes are composed of patch mosaics. From Reynolds et al. (1997).

horizontal perspective focuses attention to the spatial distribution of, and interactions among, system components (Rowe 1961). In Woodcock and Harward's scheme for forest landscapes, each object in the hierarchy has relevant factors that are important in functioning at each particular scale, e.g., land use and fire history are important at the forest stand level, light availability is critical at the individual tree scale for recruitment, and carbon dioxide concentration affects photosynthesis at the leaf level. In Reynolds et al.'s hierarchy, the behavior of an individual patch is determined by the functional and structural properties of the plants (vertical perspective), and interactions of the plants with their immediate abiotic and biotic environment. The behavior of a patch mosaic is a function of its composition, configuration, and dominant flow paths (horizontal perspective). These structural characteristics are key in determining the functioning of a particular mosaic in aridlands, e.g., the effect of vegetation on hydrologic flow, seedling establishment, and exchanges of water, organic matter, propagates, nutrients, sediments, etc. (see review in Reynolds et al. 1997).

In Table 14.3 we show a nested hierarchical scheme developed by Reynolds et al. (1996) for integrating horizontal and vertical perspectives in arctic tundra landscapes in Alaska. The smallest landscape spatial unit is at the scale of an individual plant. The functioning of plants is determined by the strength of couplings to the environment via numerous plant–soil–atmosphere–animal vectors. At the next level, plants plus soils, microbes, animals, etc. comprise "patch" ecosystems, which are relatively discrete and internally homogeneous. At the next level, a series of connected and inter-related patches may take a number of different spatial configurations, e.g., necklaces, spiders, meshes (see Figure 14.5). In tussock tundra landscapes on the North Slope of Alaska, variegated necklaces tend to predominate (Reynolds et al. 1996; Shaver et al. 1991; Walker and Walker 1996). Field studies at the level of flow paths correspond to examining the degree of "connectedness" between patches, which is critical since ecosystem processes are directly affected by transfers of materials across system boundaries. Typically, water, atmospheric turbulence, and animals are the main vectors of transport of material and energy between patches (Table 14.3). The next level in Reynolds et al.'s hierarchy is the landscape, which is viewed in hydrological terms as an "integrated flow system." An integrated flow system is the assemblage of individual plants, patches, and flow paths that deliver mass and energy (mainly by gravitational processes) to a "distribution flow line" or stream and respond similarly when subjected to a precipitation event. Movement of mass along flow lines is distinguished from flow paths in that the former is not between adjacent patches. The largest landscape spatial unit is a region, which is a mixture of integrated flow systems that make up the scale of interest. The landscape spatial units in Table 14.3 illustrate both vertical (functional) and horizontal (structural) components of landscapes and, via the various coupling vectors, these exist as interactive hierarchies. While one may argue about whether these units are inherent entities or results of interactions between human perception and the objective world, in either case explicitly identifying these hierarchical levels is essential in order for us to simplify and understand functioning in complex landscapes.

Table 14.3 Landscape spatial units (LSU) and associated water, energy, and nutrient functions used to model arctic landscapes. Modified from Reynolds et al. (1996).

	Structure		Function and coupling vectors	
LSU	Spatial scale[a] (m^2)	Typical Components	Water	Energy/Nutrients
Plant	10^{-4}–10^{-1}	• Leaves • Stems • Roots • Soil volume	• Soil water • Transpiration • Water uptake	• Photosynthesis • Respiration • Nutrient uptake • Herbivory
Patch	10^{0}–10^{4}	• Plants • Soil • Microbes • Animals	• Precipitation • Infiltration • Run-off • Evapotranspiration • Soil water	• Net carbon balance •Nutrient cycling •Decomposition •Trace gas flux
Flow path	10^{2}–10^{5}	• Patch ecosystems • Connectivity patterns (see Figure 14.5)	• Soil water flux and discharge [Hillslope Darcian flow dominant]	• Mass flux of sediment • Mass flux of dissolved nutients • Aeolian transport
Landscape (= Integrative flow system)	10^{6}– 4×10^{6}	• Flow path ecosystems • Groundwater; channel storage		
Region[b]	10^{7}–10^{10}	• Landscapes (= Integrative flow systems); lakes; rivers	• Channel flow [Turbulent flow dominant]	• Hydrologic transport of sediments • Hydrologic transport of dissolved nutrients • Aeolian transport • Migration

[a] Examples of "typical" values based on Osmond et al. (1980), Woodmansee (1990), and Walker and Walker (1991).

[b] "Mesoscale" in Walker and Walker (1991), which includes second-order watersheds.

Hierarchical Patch Dynamics

Since the late 1970s, patch dynamics has gradually been recognized as a general conceptual framework for ecological studies at different levels of organization, facilitating the integration of the horizontal with vertical perspectives. Recent developments in hierarchy theory, on the other hand, have elevated the vertical perspective to a new level of sophistication that recognizes the multiplicity of scale. One of the most significant contributions of hierarchy theory is its role in making researchers acutely aware of the importance of scale (O'Neill 1996) (see discussion below). The structure, function, and dynamics of complex landscapes are determined by individual patches and their interactions at — and usually across — different hierarchical levels. Given the nature of patches — and the causes and mechanisms of patch formation described above — we can view ecological systems as hierarchical, dynamic patch mosaics. The hierarchical patch dynamics paradigm (HPDP, Wu and Levin 1994; Wu and Levin 1997; Wu and Loucks 1995), which explicitly integrates hierarchy theory (Pattee 1973) and the patch dynamics perspective, enhances understanding pattern–process–scale relationships in landscapes by providing both an organizational and operational framework. The main elements of HPDP include:

1. *Ecological systems may be viewed as nested hierarchies of patch mosaics with discrete levels.* In contrast with the traditional individual–population–community/ecosystem hierarchy, HPDP takes a naturally defined spatial unit — the patch — as a structural and functional unit that is scale and process dependent.
2. *Dynamics of ecological systems may be viewed as the composite dynamics of interactive patches at different (usually adjacent) hierarchical levels or scales.* Phase changes of individual patches at local scales and pattern changes of patch mosaics at broader scales, as constrained by higher levels, together give rise to system dynamics. For example, the dynamics of a regional landscape may be understood as the result of the dynamics of its nested components, various ecosystems, and the exchanges of energy and materials among them via topographical, hydrologic, and other physical and biological processes. In general, higher levels impose top-down constraints to lower levels by having slower or low frequency processes, while lower levels provide mechanistic explanations for and give apparent integrity to higher levels through active interactions among components (holons). Thus, one can only see the meanings of lower-level processes at higher levels, and understand mechanistically higher-level phenomena by examining lower levels.
3. *Pattern and processes are reciprocally related, and both of them and their relation are also scale dependent.* Pattern — be it spatial or temporal — is inseparable from scale. Different patterns and processes are usually distinctive in their characteristic scales at which they operate. The challenge is to identify these scales, and properly link processes and patterns.

4 *Nonequilibrium and stochastic processes are predominantly common in ecological systems over different scales.* To understand and predict ecological dynamics, transient phenomena (frequently at finer scales) must be considered. For example, variability often is more insightful than means. Also, nonequilibrium and stochastic processes do not necessarily negate stability (see below).

5. *While homeostatic stability essentially does not exist in ecological systems (except individual organisms), persistent ecological systems usually exhibit metastability (homeorhetic, quasi-equilibrium states).* An important mechanism of achieving this metastability in hierarchical systems is incorporation, whereby nonequilibrium patch processes at one level translate to a quasi-equilibrium state at a higher level. For example, the steady state dynamics at the landscape

> level may be composed of transient dynamics at the component ecosystem level such as in the case where long-term fire patterns may consist of many short-term destabilizing forest fires. In contrast to the stability that derives from an assumed self-regulation in a closed system, the concepts of incorporation and metastability emphasize multiple-scale processes and the consequences of heterogeneity.

The HPDP has several implications for modeling complex landscape models (see Wu 1999). First, a landscape can be modeled as a spatially nested hierarchy composed of patch ecosystems as in the examples shown in Figures 14.6–14.8. The spatial patches are defined based on natural boundaries (e.g., soil types, topography, hydrologic units, or disturbance regimes) at a particular scale (or range of scale) where most, if not all, processes of interest respond. Different processes will operate at different characteristic scales, which in turn dictate the average size of patches relevant to them and thus give meanings to patchiness at respective scales. Hierarchy theory also suggests that ecological systems are, but only, near-decomposible (Pattee 1973; Wu 1999). Conceivably, different ecological systems may have different degrees of decomposability. In general disaggregation errors should be expected when systems are modeled hierarchically.

Second, hierarchy theory suggests that only three levels (or scales) usually are necessary to be considered in a model in lieu of completeness and parsimony (e.g., O'Neill 1988). However, there are exceptions to this general rule where effects at one level can penetrate through several levels above or below (see O'Neill 1988). It is conceivable that one may be allured to include more levels in one model due to, for example, ample data existing at finer scales. However, increasing the number of levels in model usually leads to greater model complexity, which reduces its comprehensibility and explanatory power and introduces a number of other potential sources of errors (parameter estimation, etc.) (Reynolds et al. 1993).

Third, it is not necessary (and not ecologically defensible in most cases) to assume the existence of a stable equilibrium when one builds a model to simulate a landscape system that appears to be stable. Indeed, assumptions of equilibrium and homogeneity may have hindered our understanding of spatially complex ecological systems (see discussion in Wu and Loucks 1995).

Hierarchical Modeling Approaches to Landscape Function

At all scales, the structural and physiological properties of patches will be different. Hence, we expect that functional attributes — such as carbon dioxide and water vapor fluxes — will differ from one patch to another (Jarvis 1995). If we were able to measure functional attributes for each patch simultaneously, simply adding them up would provide total landscape estimates. This is probably impractical at present for very large, complex landscapes. Using some of the experimental methods described in Valentini et al. (this volume), estimates of net ecosystem exchange (NEE) may be taken at different scales (patch to landscape) using towers or aircraft-borne instrumentation. Jarvis (1995) provides a thorough overview of these and other experimental methods as well as some of the compromises involved in trying to scale experimental results up to a landscape by summation, averaging, and aggregation.

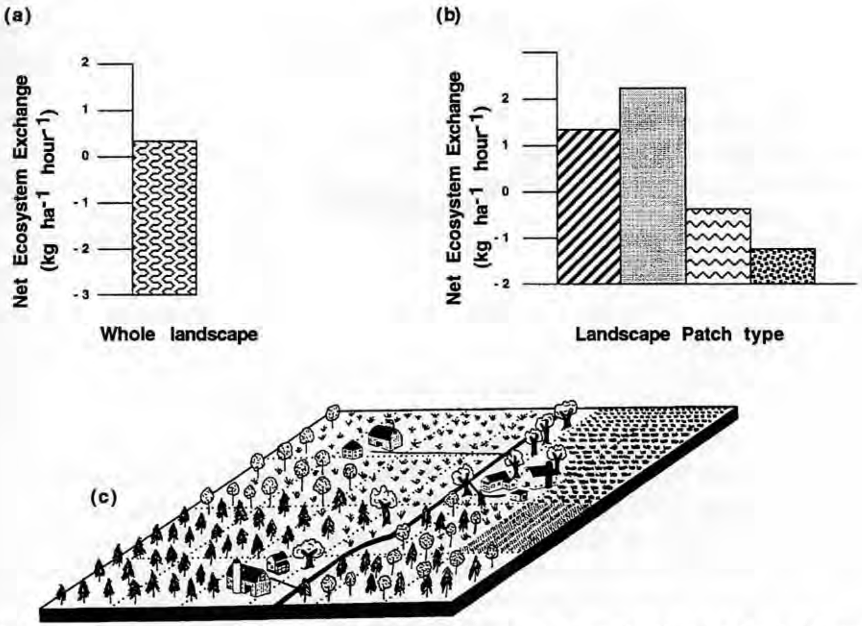

Figure 14.9 Three types of models of landscape change, distinguished by their level of aggregation: (a) Non-spatial, patch implicit, (b) Quasi-spatial, patch explicit, and (c) Spatially explicit. Modified and redrawn from Baker (1989).

How we model landscape function is dictated by how much structural detail we want to consider, that is, by the level of "lumping" or aggregation attempted. We distinguish three general types of models (modified from Baker 1989). *Non-spatial, patch implicit* models are those that ignore spatial structure and attempt to model some landscape variable in aggregate, e.g., NEE (Figure 14.9a). These are traditional point models used in population, community, and ecosystem ecology but applied at a larger scale. *Quasi-spatial, patch explicit* models (e.g., partial differential equation models with inner-patch dynamics) are models that include more details of the landscape, such as the relative contributions of each patch type to the modeled variable of interest (Figure 14.9b). *Spatially explicit* (including raster and vector based) landscape models are the most detailed: they consider explicit spatial locations and configurations of the patches (Figure 14.9c). Both nonspatial and quasi-spatial models may be submodels of the spatial landscape model, depending on the degree of detail incorporated. In this example, as more and more details are added, estimates of NEE as a function of patch configuration and environmental driving variables may be improved, but we must determine how to scale these results to larger landscapes.

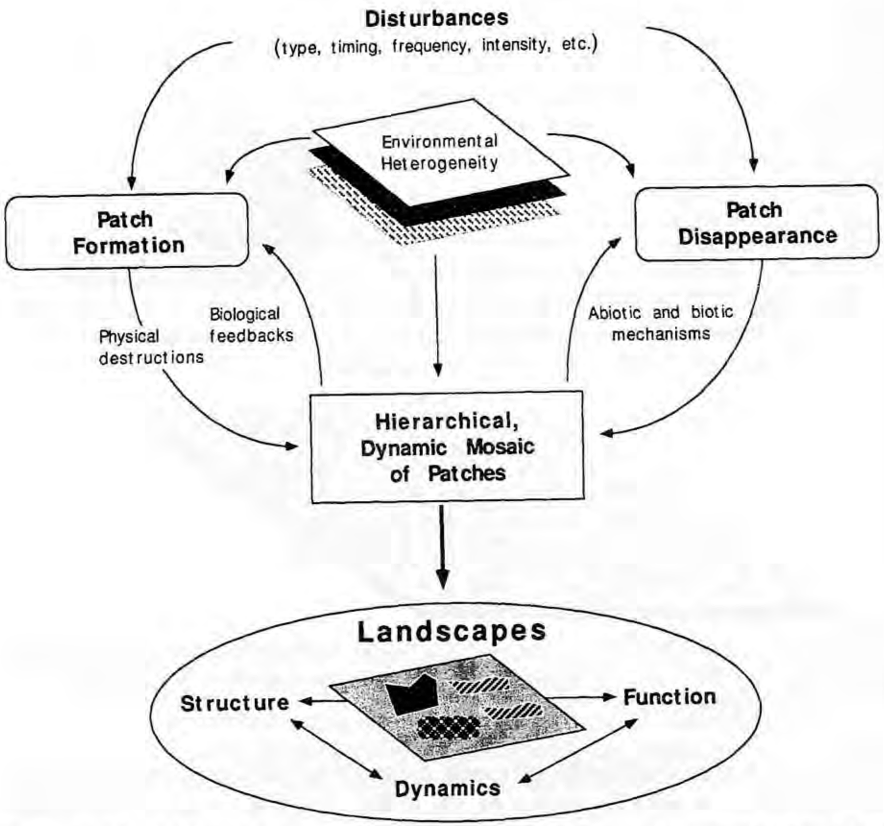

Figure 14.10 A hierarchical patch dynamics modeling framework, illustrating how patch-level processes scale up to the landscape level. Redrawn from Wu and Levin (1997).

A general bottom-up hierarchical approach to modeling patchy ecological systems involves accounting for the dynamics of pattern and processes on different levels (e.g., local patches, patch aggregates, and the landscape). By incorporating pattern and processes that operate on larger scales, these local patch models can be scaled up to a landscape-level patch dynamics model (Figure 14.10). Although this conceptual framework holds for many systems and is useful to model-building, the biological connotation of patch dynamics and mathematical details may vary greatly depending on questions to be addressed. This conceptual framework is evident in many spatially explicit landscape models (Baker 1989; Wu and Levin 1994, 1997).

Finally, we present an example of HPDP from Reynolds et al. (1993) of a "three-level-chain" hierarchical modeling scheme to illustrate how mechanistic information at lower hierarchical levels may be used at higher levels via a "filtering" or simplification process. The goal was to examine *stand* level responses of chaparral ecosystems to altered resource availabilities, e.g., nitrogen (N), solar radiation, carbon dioxide, etc. Reynolds et al. used a mechanistic plant growth model (GePSi), parameterized for various chaparral species, to predict maximum relative growth rate (Rmax) of these species as a function of light, CO_2, and N. Simulations of GePSi (daily time step) were conducted for a wide range of resource availabilities to calculate a response surface for Rmax, from which a simple hyperbolic model was then fit. Next, this empirical function for Rmax was substituted into PHENPLT, a simple phenomenological model of plant growth contained in STAND, a community model of long-term (annual) stand dynamics of chaparral ecosystems. In the original version of STAND, Rmax was fixed and not responsive to changes in resource availabilities; although the new Rmax is an empirical function of CO_2, solar radiation, carbon dioxide, and N it was developed from data generated by GePSi, which is a detailed model with high extrapolation potential. Stand level effects of altered resource availability could not have been investigated in the original version of STAND because plant growth responses to resources were not represented. On the other hand, population and community effects of resource availability could not be addressed by GePSi since community level processes like mortality and competition among plants are not included. Each model (GePSi and STAND) is best at answering questions at its own level of focus. The HPDP approach described here permits us to include information from a mechanistic model at a lower level in the hierarchy into a model at a higher level without directly incorporating the complete model structure. Following a similar hierarchical approach, Williams et al. (1997) developed a model to predict terrestrial gross primary productivity in diverse environments and ecosystems based on a more detailed model.

SUMMARY

In the **INTRODUCTION**, we noted the many gaps in our current understanding of hydrologic, ecosystem, and biogeochemical processes in complex terrestrial landscapes. This lack of understanding presents an interesting paradox. On one hand, while empirical studies cannot possibly provide the necessary understanding — which suggests a central role for modeling — the paucity of data also suggests that it is premature to develop integrated models of complex landscapes. There is a danger that in the absence of understanding, untested hypotheses can easily become incorporated into models (and then forgotten) and important processes that operate at various levels of biological organization are ignored with unknown consequences.

On the other hand, we have no choice since the questions being posed by resource managers and government policy-makers at local, regional, and global scales require the development of such integrated models. Consequently, models must represent an uneven blend of "state-of-the-art" knowledge and numerous assumptions, which are based on both practical and theoretical considerations and guesses. By linking these models with emerging technologies like remote sensing and geographical information systems, it will be possible to simulate complex scenarios of environmental–biotic interactions under differing sets of assumptions. As our knowledge improves, these models will improve, although numerous pitfalls exist since model testing and validation will often be inadequate or impossible at broader spatial and temporal scales.

In this chapter, we have argued that complex landscapes have structural and functional units at different scales. This argument is based on both theoretical and empirical evidence. According to the hierarchical patch dynamics paradigm, landscapes can be perceived as near-decomposable, nested hierarchies, in which hierarchical levels correspond to structural and functional units at distinct spatial and temporal scales. We have presented examples from a range of systems that seem to support the existence of these units. The process of identifying structural and functional units involves finding the characteristic scales of ecological processes of interest and decomposing landscape systems. The objectives of doing so are twofold: (a) to simplify the complexity of landscapes by providing a hierarchical structure to them, and (b) to promote multiple-scale approaches by emphasizing the equal importance of top-down constraints and bottom-up mechanisms. While simplification is the key to achieving understanding, the consideration of scale multiplicity in studying complex landscapes is dictated by the hierarchical properties of landscapes. We believe that the hierarchical patch dynamics paradigm provides a conceptual framework to accomplish these two objectives. We also have discussed how to use this paradigm to guide model building of landscapes by presenting a general hierarchical patch dynamic modeling approach. While this approach has been used in landscape modeling in recent years, its potentials and pitfalls, especially when used for developing integrated landscape models, are yet to be explored.

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15

Effect of Landscape Fragmentation, Disturbance, and Succession on Ecosystem Function

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ABSTRACT

Landscapes are mosaics of patches each with potentially different effects on material flows and balances. Thus, net material fluxes are dependent on the structure and pattern of landscape units. Landscape pattern derives from both exogenous factors, such as topography and soil types, and endogenous factors, such as spatially correlated disturbances, propagule dispersal, and the material flows themselves. If we aim to describe and predict the role of landscapes in moderating material flow under changing conditions, it appears that models of landscape processes are likely to be a greater limitation than data availability per se. Even simple models show that self-generated patterning within a landscape can have major effects on the predicted dynamics of the communities within it and the associated fluxes. There is some progress towards developing rules for particular phenomena associated with landscape processes but these rules are far from forming an integrated set. The challenge in developing models of the complexity of landscape processes is to separate those components that affect the phenomena of interest from those that are noise. Hierarchy theory has provided some helpful insights into how to do this but there is still no clear hierarchy of spatial and temporal scales that link the patch to the global scale via landscapes.

INTRODUCTION

We live in landscapes; we manage landscapes. We often describe the environment around us in terms of landscapes. Yet landscapes have long been a scientific blind spot (Figure 15.1). The scientific description and classification of landscapes is weak and our understanding of their role in ecosystem functioning is poor. In this chapter I ask,

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Integrating Hydrology, Ecosystem Dynamics, and Biogeochemistry in Complex Landscapes
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