Standing, left to right:
Will Steffen, Jim Reynolds, Jianguo "Jingle" Wu, Harald Bugmann, Pavel Kabat, Jean-Claude Menaut
Seated, left to right:
John Aber, Basil Acock, Ian Noble, Indy Burke

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Group Report: Hydrological and Biogeochemical Processes in Complex Landscapes — What Is the Role of Temporal and Spatial Ecosystem Dynamics?

J.D. ABER and I.C. BURKE, Rapporteurs

B. ACOCK, H.K.M. BUGMANN, P. KABAT, J.-C. MENAUT, I.R. NOBLE, J.F. REYNOLDS, W.L. STEFFEN, and J. WU

INTRODUCTION

The effects of landscape complexity, including the dynamics of the landscape pattern itself, have often been neglected in studies of ecosystem functioning. Most studies of atmospheric exchange processes with the land surface and of biogeochemical cycling in complex landscapes have assumed that the pattern of the landscape (e.g., vegetation mosaic) is constant. The question has been to determine how a given landscape pattern affects flows and pools of material and energy. However, the assumption of a static landscape pattern can no longer be made. Given the speed at which humans are converting or modifying landscapes and the need to consider decadal (or longer) time scales in the context of both sustainable development and global change, the questions discussed by our group have become increasingly important. How does landscape pattern itself change? What processes drive these changes in complexity? How do such changes interact with the functioning of the landscape? How can we improve our understanding of the changing complexity of landscapes? How can we describe the interactions between process and pattern in landscapes when both are changing, on varying time scales?

The specific objectives of our discussion group were: (a) to prioritize the ecological processes that drive change in landscape pattern; (b) to review current landscape

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modeling, experimental, and observational approaches (with a focus on modeling); and (c) to explore ways in which these approaches can be developed towards a more complete integration with hydrological, biogeochemical, and atmospheric exchange process studies.

PATTERN AND PROCESS AT LANDSCAPE TO REGIONAL SCALES

Over the past decade, considerable interest has developed in understanding and assessing ecosystem dynamics at landscape to regional scales (e.g., Peterjohn and Correl 1984; Lajtha and Schlesinger 1988; Pielke and Avissar 1990; Aber et al. 1993, 1995; Groffman et al. 1988, 1992, 1993; Burke et al. 1990, 1991, 1997; Lindner et al. 1997). Landscapes and regions are the composite units of relevance for scientists addressing global-scale dynamics, or seeking to assess global biogeochemical and hydrologic budgets and the interactions between biospheric and atmospheric dynamics. In addition, landscape to regional scales approximate the areal extent of management and political units.

For the purposes of understanding and assessing biogeochemical, energy, and hydrological fluxes, what are the key ecosystem variables that are important to study at landscape to regional scales? There are two kinds of ecosystem attributes that we may consider here: the actual processes of interest, and the structural and functional attributes needed to calculate or assess those processes.

The key processes at landscape to regional scales include the net atmospheric exchanges of CO_2, H_2O, trace gases including N_2O, NO, CH_4, and hydrocarbons, nutrient input via wet and dry deposition, lateral transport of nutrients via the hydrologic cycle, and atmosphere–biosphere energy exchange. There are also ecosystem processes that are of primary interest to managers at landscape to regional scales. Many of these are summarized in Daily (1997) and include natural resource production such as timber, grain, forage, and livestock yield, which are closely associated with primary and secondary productivity.

Structural attributes over the landscape or region that are necessary to determine these key processes include topography, soil mineralogy, vegetation composition, leaf area index, surface roughness, albedo, primary productivity, and respiration, insofar as they influence net ecosystem production (both primary productivity and respiration), evapotranspiration, percolation, overland flow, and microbial processes responsible for trace gas fluxes. In addition, information regarding land-use management practices such as harvesting history, cultivation, fertilization, and crop types may be crucial for assessing large-scale ecological functioning (Cohen et al. 1996; Burke et al. 1991). These criteria apply to the study of individual sites or plots as undertaken in traditional ecological or ecosystem research. However, placing these sites in complex landscapes implies that transfers across plot or unit boundaries are important and that they affect the dynamics of all units.

Landscapes are four-dimensional systems with considerable complexity in the spatial domain: in addition to within-plot dynamics, as measured in traditional studies, placing these sites in complex landscapes assumes that transfers across plot or unit boundaries is an important process that affects the dynamics of the unit. The vertical transfer of materials is important in integrating landscapes with the atmosphere and broader biogeochemical cycles, adding a third dimension. Finally, the representation of landscapes as dynamic, with the status and distribution of the basic landscape units changing over time, defines the fourth dimension. Considering the full range of interactions and feedbacks between processes, landscape units, and adjacent atmospheric and hydrospheric systems, the complexity of this approach becomes apparent.

Adjacency, Self-organization, and Thresholds

One of the major tasks that distinguishes landscape ecology from other environmental disciplines, and which lends complexity to its practice, is understanding and representing the phenomena that arise from and are associated with the adjacency of the landscape elements. One implication of the recognition of adjacency effects is the potential for positive feedbacks affecting these transfers, resulting in increasingly complex and nonrandom distributions across the landscape. The tendency toward self-organization creates important breakpoints in the dynamics and distribution of ecological characteristics. These three issues will be discussed below.

Adjacency

Adjacency is important wherever there are significant transfers of material, energy, or information between adjacent patches. Adjacency itself is scaled differently for different processes. The transport of materials by mass flow is usually between directly connected patches (e.g., Peterjohn and Correll 1984), while for the transport of propagules, adjacency is defined by a wider neighborhood (e.g., Coffin and Lauenroth 1989). Spatially correlated events, such as fires, disease outbreaks, and landslides, are important phenomena in which adjacency is significant (e.g., Turner and Romme 1994).

Adjacency has usually been incorporated in models of landscapes by adopting pixelated, or less commonly, polygonal representations of the horizontal structure (Costanza et al. 1990; Keane et al. 1996). More formal mathematical representations, such as fields and diffusion gradients, have sometimes proved useful for investigating components of complex systems, but have proved to be of limited value in more comprehensive models (Wu and Levin 1994, 1997). Both the pixelated and polygonal representations usually require some form of classification of the landscape elements into a discrete number of groups. The issue of general classification schemes of landscape elements has not been fully resolved in landscape ecology or modeling (see section on **LANDSCAPE FUNCTIONAL TYPE**).

There are no models that have successfully incorporated all of the important biological (e.g., propagule dispersal, animal movement), biogeochemical, and disturbance flows in a single system. The main challenge is that different processes are optimally represented at different temporal and spatial scales. Integrating across a variety of scales within a single model remains a challenge awaiting solution.

For some tasks, a complete representation of all processes at optimal resolutions may not be essential. For example, in many of the interactions with the landscape, atmospheric processes integrate over scales of several kilometers (Pielke et al. 1997), and finer-scale representations of structure and function (e.g., biogeochemical processes) may not be essential. Models are now being developed that take advantage of this observation, such that at regional scales, mesoscale circulation models are being linked to ecosystem simulation models to represent the interactions among landcover, biogeochemical, and atmospheric processes (Pielke et al. 1993). At larger scales, the same types of frameworks are being developed through linkages of the DGVMs (Dynamic Global Vegetation Models) and General Circulation Models (GCMs). However, simplification is not straightforward. Most processes are nonlinear and are affected by numerous stochastic (and possibly chaotic) phenomena, so great care must be taken in averaging over smaller scales.

Self-organization

Self-organization in a landscape occurs when a process or event establishes a pattern in the landscape, which is then reinforced by subsequent processes induced by that pattern (Holling et al. 1996). For example, in semi-arid systems, a sparse and patterned distribution of shrubs establishes localized patches into which nutrients are concentrated by plant uptake from the surrounding bare ground and by deposition in the patch as litter, as well as by entrapment of airborne particles (Charley and West 1977; Burke et al. 1989; Schlesinger et al. 1990). Increasing redistribution of resources from plant interspaces to under shrubs may lead to shrub-associated dune formation and the persistence of shrubs in the same location in the landscape (Schlesinger et al. 1990). Another example is the introduction of pattern into an initially homogeneous landscape by disturbances such as fire or landslide (Romme and Despain 1989; Turner and Romme 1994). Subsequent distributions of plants and changes in structural components of the resulting patches can increase the chances for another disturbance of the same type (e.g., a moist forest is converted to a grassland that dries more rapidly), further reinforcing the initial disturbance-derived pattern. Thus, the original patch distribution tends to persist for very long periods. Self-organizing disturbance can also take the form of moving fronts of vegetation decline and regeneration such as in the fir waves of high elevation temperate mountain systems, in which a disturbed edge increases wind-stress and desiccation along this edge, leading to continued mortality along that edge, and the development of a mortality "wave" (Sprugel 1984). The effect of self-organization on the study of landscapes is that point models which do not include adjacency effects will not capture a primary process controlling the distribution

of pattern and function over those landscapes, and hence will not provide an accurate representation of landscape phenomena.

Thus, there are three general classes of conditions that tend to lead to large adjacency effects and self-organization in landscapes: (1) places with dynamic geomorphology (e.g., landslides, river channels), (2) where limiting resources exhibit high mobility between patches (semi-arid systems), and (3) where disturbance creates subsequent pattern in vegetation which increases the chance of repeated or continuing disturbance (fire and fir wave examples). Self-organization may be present in most systems but is not an obvious factor in all of them. Strong environmental gradients tend to override the tendency towards self-similarity of adjacent patches but self-reinforcing patterns may still be present. Where a process tends to rehomogenize the landscape (e.g., very extensive fires or droughts), there will be little opportunity for self-organization to arise.

Important feedbacks can also be introduced through effects of landscape pattern on atmospheric processes. Mesoscale climate models have shown that nonhomogenous distributions of vegetation types within a landscape (e.g., fields or burned areas adjacent to forests) can result in very significant increases in the total amount of precipitation received in a landscape area, as well as highly nonhomogeneous distribution of that precipitation (Pielke and Avissar 1990). The general effect of this feedback is to increase precipitation in the drier parts of the landscape, providing a negative feedback on the inhomogeneity of soil moisture. There may be potential in these landscape level studies of vegetation–atmosphere interactions to understand the effects of different patterns of land use on mesoscale climate such that, for example, patterns of clearing in tropical forests could be designed to minimize local climatic effects. The DGVMs mentioned above are designed to increase the realism of these feedbacks for GCM-scale modeling.

Thresholds

Essentially, self-organizing processes will tend to maintain landscape units within a specific condition until a sufficiently destabilizing disturbance pushes that patch into a different state. Thus, patches that appear stable over long periods of time may be "pushed" into a very different state by a single disturbance event. Self-organizing processes may then tend to maintain that new state. The boundary between these states is the threshold condition.

Some landscapes are mosaics of patches representing different sides of a threshold. For example, savannahs can switch between grass- and tree-dominated states, and discrete disturbance events can move patches between these two states. In general, patterns generated by ecotones between systems dominated by different physiognomic groups of plants are candidates for important threshold effects (e.g., forest–prairie border, alpine treeline, taiga–tundra border).

Major disturbance events may also push otherwise stable landscape units across thresholds and into new states (e.g., Zobel and Antos 1997). Examples could include major erosional events, volcanoes, extreme fires, and altered groundwater depth. Some of the most severe threshold effects are associated with human land use. Conversion of land from forests to croplands and pastures as well as from agricultural land to urban-suburban and industrial land are extreme and often nonreversible (due as much to social as to ecological constraints). Our ability to predict future changes in patterns of human use of the landscape is very limited, and feedbacks between altered land use and climate models are not fully recognized. For example, extensive conversion of forest land to crops and pastures could alter land-surface albedo in a way that would lead to large climate changes, both locally and globally (Pielke and Avissar 1990; Pielke et al. 1991). Such changes could be greater than the effects of global-scale changes in radiative forcing by increased trace gas concentrations.

Indicators of Landscape State

Given the difficulties of understanding and modeling the complex interactions resulting from adjacency, self-organizing, and threshold effects, short-term analyses and monitoring of landscape status may require the development of simple, robust indicators. If landscapes are concrete entities, they can be characterized by indicators that summarize a larger or more complex set of information or that capture some of the emergent properties. Such indicators should ideally be readily measurable, repeatable, should be directly related to important ecological processes or conditions, and should integrate over space and/or time. Examples might include river nitrate concentrations, albedo or leaf area index, biological diversity, and other tangible and measurable indicators. A number of theoretial variables have also been suggested, such as ecotone length, indices of degree of fragmentation/contagion and connectivity, and pattern analysis (Li and Reynolds 1997); a key potential area of development is the connection between these two types of landscape indicators. As models of landscape dynamics develop, measurements of indicator variables can provide validation data for those models which span over large spatial scales.

Indicators have little value *per se* and should relate to a specific question/problem, either scientific or practical (e.g., management issues). They will be mainly considered as comparative tools, either between landscapes or between varying states of a given landscape with time. They can be simple "descriptors" of extent (e.g., total area, number of units) or more complex ones such as geomorphology and hydrological network. They can also be "integrators" and relate to structural, functional, or dynamic properties of the landscape. Some originate from ground-based measurements (e.g., water yield and nitrate concentration in streams, [Bormann and Likens 1979]) and some from space-borne instruments (e.g., albedo or foliar nitrogen concentration [Reich et al. 1997; Martin and Aber 1997]), which call for statistical methods comparing sequential scene measures.

Some indicators may be more difficult to obtain than others. As an example, for landscape architecture, such indicators may vary from ecotone length to indices of degree of fragmentation/contagion and connectivity, including pattern analysis. Though simply measured, some can derive from previous process studies and then be interpreted in relation to cross-boundary transfers or retention phenomena (sources and sinks, e.g., sediment load, chemistry of stream water).

Indicators of disturbances may constitute early warning signals (e.g., river nitrate concentration as in Cole et al. [1993], Caraco et al. [this volume], Howarth et al. [1996]) or reflect thorough changes in structure and/or function (e.g., water DOC/DON concentration, species biodiversity). Preferably, indicators should be cross-linked, thus leading to more thorough interpretation. Indicators that reflect known patterns of change in ecosystems, substantiated by experimental studies, will be most valuable.

There are other types of indicators, including those that represent system state but may not be easily measured over landscapes, and do not integrate spatially. These include biodiversity, the presence or absence of rare species in general, or of species that signify ranges of environmental conditions (e.g., the disappearance of lichens from tree bark in polluted areas). There are also measurements that are difficult to make but do integrate spatially, such as eddy covariance (e.g., Wofsy et al. 1993) or aircraft-borne measurement of total landscape gas fluxes.

LANDSCAPE FUNCTIONAL TYPES

The complexity inherent in connected landscapes suggests that a simplifying heuristic is needed in developing manageable conceptual and computer models. The most commonly proposed heuristic has been hierarchy theory (see Reynolds and Wu, this volume; Noble, this volume). Hierarchy theory is rich in conceptual approaches and provides useful prescriptions for breaking complex landscape systems into manageable levels and scales; however, to date its utility has been limited to generating broad guidelines rather than a specific and rigorous integrative structure.

Hierarchies can be described in terms of both spatial distribution and processes (O'Neill et al. 1986; Wu and Loucks 1995). For spatial distribution, a fundamental concept is that of the landscape patch or landscape functional type (LFT). An analogous concept, that of plant functional types (PFTs), has been subject to considerable research efforts and much debate over the past years (cf. Chapin et al. 1996; Woodward and Cramer 1996; Smith et al. 1997). According to the PFT concept, plants can be grouped or classified in a variety of ways, some of which are based on functional differences (e.g., photosynthetic pathways = C_3 vs. C_4) or structural ones (e.g., growth form = trees, grass, herbs). Such classifications (or simplifications) are valuable for identifying general patterns, for reduction of complexity, and for integration across different disciplines. For example, in the latter instance, PFTs are the basis of many global vegetation models. While the concept of PFTs is appealing, many approaches and philosophies have been identified, and there are a number of methodological approaches to the PFT concept (cf. Gitay and Noble 1997). Consequently, a large variety of different PFT schemes have been proposed for various purposes (Woodward and Cramer 1996; Smith et al. 1997).

In an analogous way, the concept of landscape structural and functional types (LFTs) has been proposed (see Reynolds and Wu, this volume). Like PFTs, the definition and physical meaning of an LFT will vary depending on the processes under study and the questions being addressed. In general, an LFT is an identifiable component of a landscape that represents an integrated assemblage of biological and physical entities which exchange and deliver mass and energy (via atmospheric couplings, inputs to rivers, etc.). Different LFTs operate at different characteristic scales in space and time; they are patch mosaics when viewed at finer scales and relatively homogeneous units when viewed from coarser scales. Thus, many if not most landscapes can be represented as hierarchies of patch mosaics or LFTs (Coffin and Lauenroth 1989; Wu and Loucks 1995; Wu and Levin 1994, 1997; Reynolds and Wu, this volume). Although heterogeneity occurs across scales, LFTs can be used to provide a hierarchical structure to complex landscapes so that we can focus only on a limited number of discrete scales (hierarchical levels) with insignificant loss of information. Such a simplification is necessary because (a) it is impractical to measure all processes of consideration continuously across space and time, (b) understanding is conversely related to complexity, and (c) it has been suggested that both physical and ecological processes tend to operate at characteristic scales and thus a hierarchical approach with LFTs should facilitate properly matching scales and integrating ecological with physical processes across complex landscapes.

Recognition of the boundaries of patches is not a well-developed technique. For structural characteristics, spatial statistics of two-dimensional surface distributions have been used. There have been few attempts to determine LFTs based on processes, although the identification of a given area of "homogeneous" landscape is inherent in many techniques. An example is eddy covariance, where the assumption of homogeneity within the footprint of the tower is critical, and one for which rigorous analyses are not available. Most plot-based methods also assume homogeneity within the plot; however, this is generally more easily supported for 1–10 m units than for the landscape. One method for calculating the size of the LFT for biogeochemistry studies is through the spatial divergence term (see Raupach et al., this volume). Essentially, the ratio of the divergence of the horizontal flux of mass or energy to the divergence of the vertical flux, or the vertical flux plus internal production and consumption terms, should not exceed an established critical value. Thus LFTs for nitrogen-cycling studies would be much smaller within a given landscape than LFTs for carbon balance. Regardless of the size of the LFT or the method used to determine it, land-surface parameters must be aggregated to the size of this unit. The effect of using an inappropriate patch size in a landscape-scale study of hydrologic or biogeochemical processes is unknown; however, in general, using too large a patch size will lead to errors in systems where nonlinear processes operating at sub-patch scales are important.

In studies where remote sensing data layers form an important part of the information content of the work, pixels instead of patches tend to be the fundamental landscape units used. Pixels may represent an invariant basic spatial unit that can change state through time. It is possible to combine adjacent pixels with similar characteristics into larger polygons which can then be used with landscape pattern statistics, thus combining continuous and discrete methods of spatial analysis. Mathematical treatments are better developed for discrete than for continuous descriptions of the landscape.

In addition to hierarchies of structure and distribution, complex systems can be thought of in terms of hierarchies of processes. A method for structuring models to reflect this hierarchy of processes is described in the next section.

INTEGRATING ECOSYSTEM DYNAMICS WITH HYDROLOGY AND BIOGEOCHEMISTRY AT LANDSCAPE SCALES

Ecological Models Applied at Landscape to Regional Scales

In this chapter, three types of models are distinguished that have been applied to study landscape-scale dynamics of ecosystems: patch scale models and DGVMs, both of which typically ignore interactions between neighboring patches or "pixels," and landscape models *sensu strictu*, which take these interactions into account.

Patch Models

Patch scale models that have been applied at landscape to regional scales can be classified broadly into two families: gap models and biogeochemistry models.

Gap models. The so-called "gap models" (Shugart 1984), first presented over 25 years ago (Botkin et al. 1972), simulate the competitive dynamics between individuals of different species on patches that have an area of 100–1000 m^2. These patches are supposed to be small enough so that all trees can be assumed to interact with each other. Patch-level descriptions of environmental conditions defining the light, nutrient, temperature, and water regimes of the site are used to drive establishment, growth, and mortality routines (Shugart 1984). Initially conceived as a simple four-dimensional description of the species' niche, gap models have increased considerably in complexity over time (cf. review by Bugmann et al. 1996).

While the treatment of vertical canopy structure (e.g., Botkin et al. 1972; Prentice et al. 1993), internal nutrient cycling (Pastor and Post 1986; Aber et al. 1982), and vertical water fluxes (e.g., Solomon 1986; Prentice et al. 1993) is treated in some detail in most gap models, the interactions between patches, i.e., the horizontal flows of energy, matter, and/or information, are neglected in all models except those originating from ZELIG (Urban et al. 1991). Gap models have been fairly successful in simulating species succession over time for individual "sites" (or, in the ZELIG case, small areas); however, these models are too detailed to be run with full spatial coverage for areas larger than a few dozen km^2 (e.g., a landscape of 10 km^2 is composed of 2000 patches of 500 m^2). Instead, some gap models have been applied to study regional-scale patterns of ecosystem types based on the assumption that the study area can be divided into fairly large, homogeneous units, e.g., a 10 × 10 km rectangular grid as done by Lindner et al. (1997), or a polygon-based approach derived from a geographical information systems (GIS) analysis of the model's driving variables (Bugmann et al. 1999).

Biogeochemical models. Biogeochemical models are usually structured as "box-and-flow" models describing the fluxes of energy, carbon, nutrients, and water, thereby assuming that the structure of the ecosystem is static (e.g., Parton et al. 1987; Running and Coughlan 1988). The major processes determining the rates of transfer of material between the compartments are formulated based on physiological principles, involving submodels for photosynthesis, allocation, stomatal conductance, etc.

Similar to gap models, most biogeochemistry models treat the vertical dimension in some detail, but they do not consider horizontal adjacency effects. As a matter of fact, these models have no specific areal extent and thus have been used at the plot, watershed, regional, and global level. At scales larger than the plot, they are frequently run in conjunction with a GIS to define the number and areal extent of homogeneous landscape units (cf. Pierce and Running 1995), and to produce spatially explicit outputs (Aber et al. 1995; Burke et al. 1997). Differences in vegetation composition between landscape units are summarized as changes in physiological parameters, generally representing plant functional types such as evergreen versus deciduous, tree versus grass, etc. (e.g., Nemani and Running 1996). Leaf area index (LAI) is a central driver of ecosystem processes in these models, and some biogeochemistry models aim at predicting LAI internally (e.g., Schimel et al. 1994), whereas others use LAI as an input variable derived from remote sensing (e.g., Running and Coughlan 1988).

Dynamic Global Vegetation Models (DGVMs)

Currently under development for use with GCMs, DGVMs combine descriptions of structural, physiological, and successional dynamics. In most of them, the equations are derived by considerable simplifications of existing patch-scale models, although one of the current DGVMs employs a full gap type approach. All DGVMs include biogeochemistry at the individual plant level, and most include a disturbance scheme. The vegetation is described in terms of plant functional types (e.g., C_3 vs. C_4 grasses, broadleaved vs. needleleaved trees). All climatically suitable PFTs compete for resources within a pixel, and competition rules of varying degree of sophistication are used to determine the resulting mixture of PFTs, which then is mapped as a "biome type" for that pixel.

DGVMs do not treat adjacency effects, partly due to the large size of the pixels used in global-scale applications (typically, 0.5° × 0.5°). The two major challenges facing this approach are: (a) to determine the number of PFTs required and to model how their ratio changes in the landscape, and (b) how to incorporate realistic descriptions of disturbances at these large spatial scales. By increasing their spatial resolution and

perhaps also the number of PFTs that are distinguished, it is possible in principal to apply these models at continental to regional scales.

Landscape Models

Landscape models, as defined here, explicitly address the relationship between spatial patterns and ecosystem processes, taking into account the phenomena of adjacency, self-organization, and thresholds. Most of these models are based on a gridded description of the landscape (cf. Wu and Levin 1994, 1997) and treat spatially correlated processes such as lateral flows of resources, propagules, and disturbances. The structure of these models is quite variable. Examples include Markov models and cellular automata (e.g., Gardner et al. 1996), combined Markov-cellular automata modeling (e.g., Li and Reynolds 1997), other rule-based approaches (e.g., Noble and Gitay 1996), and gap and biogeochemistry models with connections between adjacent patches (e.g., Urban et al. 1991; Leadley et al. 1996). In some cases, a hierarchy of models is used in which parameters for the simpler, low-resolution models are derived from complex models of higher-resolution phenomena (e.g., Grant and French 1990; cf. Luan et al. 1996).

In contrast to the other approaches, most landscape models treat vertical ecosystem structure only marginally but emphasize the horizontal dimension. Most of the studies using landscape models were largely theoretical, studying abstract landscapes (cf. Noble, this volume). A central challenge here is to evaluate these findings with respect to the patterns and processes in real landscapes. There are some examples of models that address this issue; however, these case studies deal mainly with water transport and employ simple routing routines and retention times within landscape units (e.g., Costanza and Maxwell 1991; Ostendorf and Reynolds 1993; Vorosmarty 1996, 1997).

Integrating Landscape-scale Models of Hydrology, Ecosystem Dynamics, and Biogeochemistry

Historically, studies of the hydrology, ecosystem dynamics, and biogeochemistry of landscapes have proceeded largely independently of each other. In each discipline, it was assumed that the variables considered by the other disciplines could be treated as constant boundary conditions. Consequently, there are only a few examples of landscape- to regional-scale studies that transgressed these disciplinary boundaries. For example, Band et al. (1993) linked a biogeochemistry model with a hydrological model for a forested watershed; over the past years, the distinction between ecosystem dynamics (gap) models and biogeochemistry models has become increasingly blurred (e.g., Pastor and Post 1986; Korol et al. 1995; Keane et al. 1996; Friend et al. 1997) because it was recognized that ecosystem structure and function cannot be treated separately, but must be considered within a single model framework. However, we are not aware of a functioning model integrating all three disciplines.

Achieving an integrated model of hydrology, ecosystem dynamics, and biogeochemistry for a given landscape could profit greatly from methodological advances like model modularity and object-oriented design, which are discussed below.

Modularity of Landscape Models

The processes of ecosystem dynamics, hydrology, and biogeochemistry are currently modeled at different temporal and spatial scales. The weather systems that drive hydrology occur at global or continental scales, ecosystems typically occupy areas of a few square kilometers, and much biogeochemistry is driven by soil microorganisms and soil conditions that vary over meters. Temporal scales are similarly variable. Previously it has been difficult to combine models over such a wide range of scales, but recently some appropriate tools have become available.

Most existing models of landscape processes have been written in procedural languages such as FORTRAN. They have described the processes operating in the system, and the state of the system has been represented by the state variables. However, many modelers are now turning to object-oriented designs (Coad and Yourdon 1990; Acock and Reynolds 1997). These designs identify the objects in the system and encapsulate in the objects both the state variables and the processes appropriate to the object. They enhance the modularity and genericness of the code, thus opening the model to contributions from many authors (Reynolds and Acock 1997). Figure 17.1 shows one possible outline for a landscape model with an object-oriented design.

With object-oriented designs, it is convenient to think in anthropomorphic terms about what the objects "know" about themselves and what processes they "know" how to perform. The objects can communicate by requesting information from each other. Thus it is possible to have objects at large spatial and temporal scales aggregating information from objects at smaller scales. For example, a landscape object might "know" that it is composed of patches and that some of these are urban, some vegetation, and some water. It might also "know" how local weather is affected by these patches, how materials move between the patches, and how to aggregate water evaporated from all the patches.

Patches can be further subdivided into vegetation types, plant types, and even individual plants if so desired (Figure 17.1). These different objects can step through simulated time at different rates as appropriate to our knowledge of the processes. Thus it is possible to develop a structure of intercommunicating objects that cover all scales of interest in the landscape. Each object can, and must, be tested individually. Such a structure will be most useful if it contains objects at all organizational levels used by the modelers who might be expected to contribute to a landscape model. It is also important that objects pass information up and down the organizational hierarchy without jumping levels. So, for example, if a plant object needs solar radiation information to calculate transpiration, and that information is a state variable in the patch, it should pass the request for the information through "Plant_type" and "Vegetation_type" to

Figure 17.1 Example object-oriented design for a landscape model.

The principal steps required to accommodate all processes discussed in the position papers are shown. Each step consists of Object_name.function_call. Successive subdivisions of the Landscape object are indented to show the hierarchy of spatial aggregation. Any or all of the steps in this structure could be expanded to give more detail and introduce additional objects.

each run:	
Simulation_controller.run	
Landscape.map_patches	Map by composition, configuration, flow paths.
Landscape.sequence_patches	Sequence based primarily on elevation.
Landscape.read_weather	Read input weather file.
Landscape.step_time	
each time step:	
Landscape.calculate_weather	Calculate effects of topography, veg. height, etc.
Landscape.sudden_change	Fire, disease, clear cutting, etc.
Land_patch.change	Change first, next, or all patches affected.
Landscape.spread_change	Propagate fire, disease to next patch. Iterate.
Landscape.call_patches_in_sequence	
Patch.step_time	Call first patch in elevation sequence
for land patches:	
Land_patch.read_weather	Get patch weather from landscape.
Land_patch.material_from_adjacent_patches	
Get materials.	
Vegetation.photosynthesize	
[Plant_type.photosynthesize	
[Plant.photosynthesize, etc. to desired level.]	
Vegetation.transpire	
Vegetation.grow	
Vegetation.species_change	Track succession dynamics
Soil.water_flux	
Soil.chemistry	
Land_patch.trace_gasses_emit	
Land_patch.expand_contract	Change map of patches.
for water patches:	
Water_patch.calculate_flow_rate	
Water_patch.sedimentation	Calculate change in sediment load
Vegetation.nutrient_uptake	
Water_patch.chemistry	
Water_patch.expand_contract	
Landscape.material_flow_between_patches	Iterate back to Patch.step_time.

the patch. Only by observing these constraints can we preserve the flexibility to integrate all contributions.

When water is the principal medium moving materials between the patches, it makes sense to calculate first changes in patches at the highest elevations in the landscape, move materials to lower patches if appropriate, then calculate changes in the lower patches. The patches are therefore sequenced for calculation according to water flow paths in the landscape. In object-oriented programming languages (OOL), it is possible to send a message like "calculate" to each patch in the sequence and have each patch know what type it is (urban, vegetation, water, etc.), making the calculations appropriate for that type of patch. This is done by using some features peculiar to OOLs (inheritance, virtual functions, and function overriding) that are not available in procedural languages (Cox 1986; Meyer 1988; Wegner 1990; Wirfs-Brock et al. 1990; Booch 1991). Thus the use of OOLs and an object-oriented design (OOD) for landscape models has distinct advantages over traditional alternatives.

PATCHES, POLYGONS, AND PIXELS

Any model that integrates all the landscape processes must be able to handle data on spatial distribution. Remotely sensed data comes from satellites as pixels, the data layers in GIS are either vector or raster representations, and other data may be collected as lists of point data with latitude and longitude coordinates. The simplest way to accommodate all these types of data in landscape models is to use a grid to represent the landscape surface, and to calculate change at each point (intersection) on the grid. This is not as computationally intensive as it might first appear. If we have already identified the patches in the landscape, we can make our calculations once for each patch and apply the results to all the points within that patch. In effect we are assuming that the square around the point is uniform. If a datum falls within the square, it is assumed to apply to the point. Using a grid of points makes it easier to represent the increase and decrease in area of the patches, e.g., when one vegetation type gradually encroaches on the area occupied by another. This encroachment is represented in the model by transferring points from one patch to another. Pixels are similar to patches because they will normally cover several points, and the model can be related to the remotely sensed data by aggregating over the points covered by each pixel. Polygons are more difficult to fit over the landscape and are rigid, i.e., cannot represent expansion and shrinkage of patches.

MODELING OVER MANY LEVELS OF ORGANIZATION

Using an OOD allows us to cover more than three levels of organization in a landscape model (Figure 17.1) when processes farther away from the level of interest have penetrating influences. An OOD allows us to treat some processes coarsely while treating others in great detail. However, there may be practical considerations such as run time. If it is desired, for whatever reason, to reduce the number of levels of organization represented in the model, this can be done by replacing the more detailed levels with empirical equations. The procedure is to run the more detailed levels of the model alone and record their responses to the input variables (e.g., Reynolds et al. 1993). Then the responses are captured in empirical equations such as multiple regression equations or neural nets. It is often possible to capture more of the behavior of objects in this way than to generate the empirical equations directly from experimental observations.

The Modeling Process

It is useful to revisit the role of simulation modeling in ecosystem and landscape to regional-scale science. Modeling represents a significant activity in these disciplines, partly because empirical analysis is difficult at these large scales, partly because simulation modeling can integrate some of the complexity inherent at these scales, and partly because of the need by policy-makers for sensitivity analyses at regional scales.

Ecosystem and landscape studies follow the general paradigm for all scientific research (Figure 17.1). The process of modeling is one of several activities that comprise synthesis. When this is the case, the set of hypotheses represented by the model must be tested against field data not used in the construction of the model or derivation of parameters ("validation"). Validation is a critical step in testing and documenting the value of any model, and it is important to use validation data that are as independent as possible from the data used in building the model.

We often learn the most when the models fail; however, such failures are rarely reported, as they are difficult to publish. This, in combination with pressure to produce a result, often leads to "tuning" or over-calibration of the model, a process in which the many input parameters in a complex model are changed until the "right" answer is obtained. Although the tuning can possibly provide insights into the model itself, these insights are rarely generally applicable to ecological systems. Instead we report on an overly fitted model whose predictions are not robust. When models fail to reproduce a validation data set, the analysis of the reasons for this failure could lead to increased understanding about the underlying ecological processes, and thus it often would increase the robustness of model-based sensitivity studies conducted under scenarios of environmental change.

Model testing at the landscape scale poses considerable, specific problems. One is the difficulty of conducting experiments at this scale, for both financial and logistical reasons, although "natural experiments" (e.g., fires or windthrow) sometimes provide opportunities for testing model behavior under contrasting conditions. It may also be possible to do experiments for only parts of a landscape, e.g., in small watersheds. Extensive transects along environmental gradients can also be useful for testing models under systematically changing conditions. The power of remote sensing to provide high resolution spatial information over large areas can be used to generate validation data sets when the error parameters of the algorithm used to convert radiance to a biophysical property are known. The limited availability of data at large scales still constitutes a major limitation to developing robust models that are aimed at assessing the sensitivity of landscapes to direct and indirect anthropogenic environmental changes.

Several examples of model validation at the landscape to regional scales have been published. These can be divided into two broad categories: (a) studies that evaluated model behavior at several to a large number of points or plots within a landscape, e.g., with respect to soil organic matter, net primary production (NPP), or the water balance and (b) spatially explicit comparisons of the simulation results with maps derived from large regional data sets, or comparisons of simulated variables like NPP with variables derived from remote sensing data, such as cumulative NDVI. For example, regional runoff maps produced by the U.S. Geological Survey and regional forest production data produced by many national forest services offer the potential for validation of NPP (Burke et al. 1991) and water yield data (Aber et al. 1995) at the landscape scale.

Given the scarcity of landscape-scale data sets, it is important to develop protocols for the standardization of methods and interlaboratory comparisons for analyses, so that data sets from other research groups and other geographical areas can be used for model testing. This is doubly important because few experiments can be performed at this scale. Some large-scale ecological studies, such as those funded by NASA in the grasslands, boreal forest, and the Amazon (Sellers et al. 1992; Sellers 1995; Hall and Sellers 1995), provide data-layer-rich spatial data sets for use in model parameterization and validation.

The power of modeling approaches in ecology could be strengthened considerably if a more rigorous modeling paradigm was applied. Today, many modeling activities in ecology are considered to be of little value by a large number of field-oriented researchers. In this context, it would be desirable to establish more rigorous criteria for reviewing modeling papers, increased expectations for validation, tighter standards for calibration, and especially a more complete presentation of the modeling process in the reviewed literature, including reports on those instances where models fail. This could increase the value of modeling as a tool for ecological analyses.

Problems in Publishing and Distributing Models

Publishing ecosystem and landscape models within the framework provided for experimental work can be difficult. Full and accurate presentation of models within peer-reviewed journals, including a complete description of model structure, a complete listing of all variables used in the model and the values assigned to each parameter, as well as the source of each value, can require substantial amounts of space and is seen as uninteresting material by some editors. It is also true that models can be most useful and informative when they fail; however, papers presenting poor agreement between measurements and model predictions are difficult to publish.

There are examples of disciplines in which a central modeling repository is provided by the professional association (e.g., groundwater hydrology modeling). With the proliferation of models at the landscape scale and the difficulty in publishing models in a format that meets the needs of the community, it is time for one of the organizations in the global change community to provide this repository and publication function.

Such a service could consist of a web-based information system in which a model code could be stored along with standardized data sets and associated outputs.

Minimal standards for documentation should be established, and the repository should be available to the entire scientific community at no cost. In association with this repository, an electronic journal should be established that would provide for peer review and "publication" of papers in electronic form only.

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