

## Dynamic spatio-temporal landscape models

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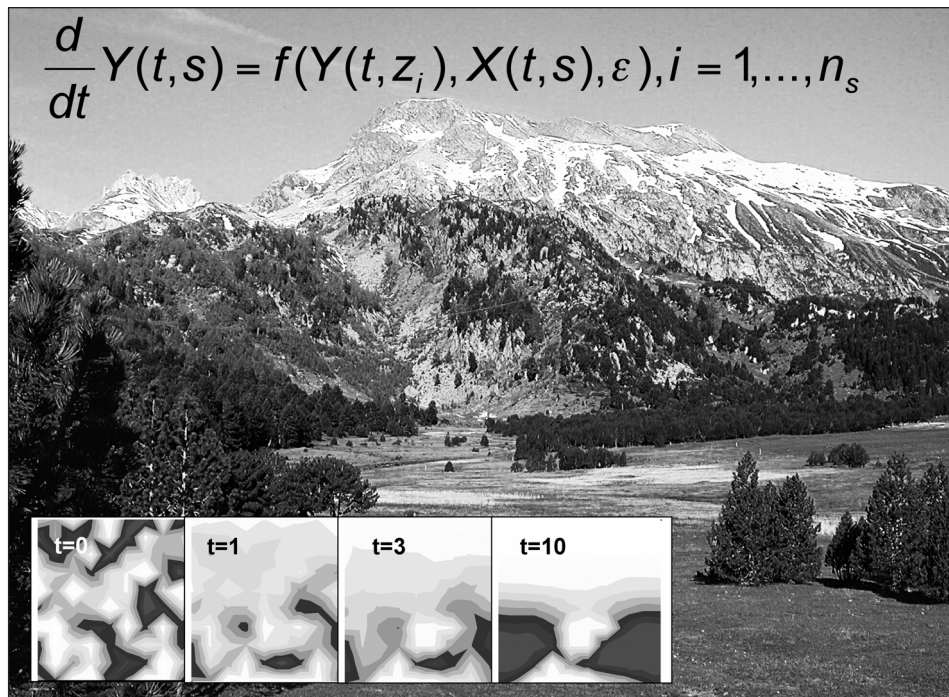
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### Abstract

Modeling at the landscape scale is most relevant to quantify and understand landscape structure and dynamics. The existing landscape models encompass static empirical models, dynamic point and area models, dynamic regionalized and spatially linked spatio-temporal (SLST) models. The latter take into account both local dynamics and spatial interactions.

This chapter discusses various SLST model concepts and approaches that are applied in landscape research. SLST models are typically used to (1) advance general ecological theory, (2) test specific landscape-ecological hypotheses, (3) run scenario-simulations, and (4) derive decision support for landscape management. We present three case studies that illustrate the use and limitations of generic and complex SLST models. In the first case study we employ SLST models to explain the formation of forest-landscape patterns. The second and third case study highlight the use of SLST models to analyze the spread of tree-species during the Holocene and to identify landscape functions for management purposes. Finally, major challenges in the field of spatio-temporal landscape modeling, scaling issues and model testing are discussed.

Keywords: landscape models, spatio-temporal modeling, spatially linked spatio-temporal models; SLST models.



## Modeling landscape patterns and dynamics

Landscape patterns (landscape heterogeneity) are the result of various drivers acting on the landscape. Drivers include exogenous factors, endogenous processes, or both (Bolliger 2005; Bolliger *et al.* 2003; Patten *et al.* 1997). In most natural systems both endogenous processes and exogenous factors influence landscape dynamics. Exogenous landscape drivers are climate, soil, or disturbances (e.g., fire, floods). Endogenous processes involve interactions between landscape elements and are usually of biotic nature (e.g., trophic interactions, competition between or within species). These interactions generate small variations between time steps and locations that finally accumulate and lead to pattern formation (Bak 1996; Bak *et al.* 1987). In environmentally extreme habitats (e.g., desert, arctic, extreme pH values in soils) landscape dynamics are likely to be primarily driven by exogenous factors. Habitats with relatively constant environmental heterogeneity between and within years (e.g., rainforests), are primarily driven by endogenous interactions (Solé *et al.* 2002; Solé and Manrubia 1995).

Interactions between the various drivers of landscape patterns and dynamics can be linear, non-linear, unidirectional or form positive (mutuality, self-reinforcing) or negative feedbacks (e.g., self-inhibition). Nonlinear and feedback interactions have been reported to be a primary source of structure or patterning in many kinds of natural systems (Bascompte *et al.* 2003; Bascompte and Sole 1995; Farkas *et al.* 2002; Green 2000). These complex interactions between endogenous and exogenous drivers of landscape patterns make intuitive understanding or direct assessments of likely cause-and-effect relationships difficult. One way to quantify and predict spatially dynamic patterns and their underlying processes at the landscape scale is to use mathematical or computer models (cf. Richter *et al.* 2002). These are implementations of conceptual models on the basis of empirical observations and experiments using the generic and uniform language of mathematics (see Seppelt (2003)). Models integrate current knowledge about interactions and influences of drivers, rank it, point to inconsistencies and uncertainties, and make simplifications explicit.

**Landscape models** formulate interactions within and between landscape elements and/or with environmental factors in space and time. By doing so, landscape models are able to relate spatial and temporal pattern to exogenous and endogenous drivers. Depending on the research question, the extents to which landscape models are applied range from one square meter to entire continents. Beyond interpretation of data, landscape models allow scenario testing by assessing various degrees of changes on a particular landscape. This may lead to confirmation, rejection, or generation of hypotheses and support environmental decisions and policy making.

In this chapter, we discuss mathematical models and computer programs that generate quantitative descriptions of landscapes in space, time or both. The chapter is an overview of a variety of landscape model approaches that are based on different model concepts, temporal and spatial resolutions, and levels of complexity. Special emphasis is given to the spatially linked spatio-temporal landscape (SLST) models.

## Types of landscape models

Although there is no generally applicable model-classification scheme, a number of model types can be distinguished based on various aspects of the modeling approach, ranging from purely conceptual, descriptive word and graphic models to semi-quantitative graphical schemes, , mathematically formalized models to computer programs yielding quantitative descriptions. These model types differ particularly in the way landscape heterogeneity is taken into account.

Often, **static modeling approaches** are the basis of large-scale spatial predictions. These approaches assume that the landscape is in equilibrium with the environment, as they do not account for transient adaptation phases. A static model  $Y(s_j) = f(X(s_j))$  links observed state variables  $Y$ , (biotic units, e.g., trees), to exogenous factors  $X$  (e.g., climate) at positions  $s_j$  in the landscape. The simulated landscape heterogeneity is thus a simple mapping of the heterogeneity of the exogenous factors. The link between state variables and exogenous factors is often performed using various regression approaches (reviews in Bakkenes *et al.* 2002; Guisan and Zimmermann 2000) ranging from logistic regression (Bolliger *et al.* 2000) to CART models (De 'Ath and Fabricius 2000), or General Additive Models (Yee and Mitchell 1991). Applied at discrete timestep(s)  $t_i$ , the model yields  $Y(t_i, s_j) = f(X(t_i, s_j))$ .

Simulations from static models thus represent the spatially detailed distributions of the biotic unit at individual timestep(s). Applications of this type of model include risk assessments of global climatic change on vegetation distribution (Bolliger 2002; Bolliger *et al.* 2000; Guisan and Theurillat 2000; Guisan *et al.* 1998), habitat suitability models for individual species (Akçakaya *et al.* 1995; Guisan and Hofer 2003; Lindenmayer *et al.* 1991), for species groups (Bonn and Schröder 2001), for communities (Peppler-Lisbach and Schröder 2004), cascades of landscape filters (Poff 1997; Schröder and Reineking 2004), or biogeographic models (Haxeltine and Prentice 1996; Holdridge 1947; Leemans and van-den-Born 1994; Neilson 1995; Prentice *et al.* 1992; Woodward and Smith 1994) for species, communities, or biomes. In these models, the variable describing vegetation, is fitted to variables expressing ecophysiological constraints, e.g., yearly day degree sum, maximum net ecosystem production (NEP) or leaf area index which can be attained under the given moisture and nutrient conditions. These vegetation models are sometimes combined with dynamic nutrient cycling models.

Advantages of static models include that they allow quick and easy calculations (regressions). Since the predictions are given in a geographically explicit form, they are interpretable as maps, e.g. in Geographical Information Systems (GIS). Spatial interactions may be accounted for by applying methods that consider spatial autocorrelation (e.g., chapter 4.2 Spatial dynamics, Augustin *et al.* 1996). Static statistical models allow assessment of factors and factor combinations that are relevant for a given landscape pattern, and are therefore in many situations a good starting point for further modeling approaches. Static models imply, however, that the ecosystems are in quasi-equilibrium, i.e. the transient behavior, the way in which the equilibrium is attained, is not accounted for. Additionally, the basic mechanisms of the spatio-temporal patterns are not explicitly included in statistical models. This limits cause-and-effect analysis and restricts extrapolations to the range of the factors (in space and time) where the model was calibrated (Lischke 2001; Lischke *et al.* 1998a; Peng 2000), as in empirical models in general.

**Dynamic models** emerge from the concept that the landscape state is defined by change, driven by exogenous factors and endogenous processes and interactions. Thus, dynamic models take the transient nature of systems into account. They are based on assumptions about the underlying processes and describe for specific localities the temporal change

( $\frac{d}{dt}Y(t)$  in continuous time or  $Y(t_{i+1}) - Y(t_i)$  in discrete time) of the state variables  $Y$  (e.g., the biomasses of tree species): ( $\frac{d}{dt}Y(t) = f(Y(t), X(t), \varepsilon)$ ). These models can be deterministic ( $\varepsilon = 0$ )

or stochastic, i.e. take into account random influences ( $\varepsilon \neq 0$ ).

A broad variety of dynamic landscape models are available. Among these, *dynamic point models* describe the dynamics of the state variables for specific locations, thus points in space through time. Dynamic point models include e.g. forest gap models (Botkin *et al.* 1972; Bugmann 2001), which simulate the establishment, growth and death of single trees on small patches and take into account the shifting mosaic of these patches created by stochastic

death and birth processes of small subpopulations (e.g., Botkin *et al.* 1970). Other approaches involve models that account for the spatial variability by using theoretical descriptions (distributions or moment equations) (DisCForM; Lischke *et al.* 1998b; Picard and Franc 2001; Bolker and Pacala 1997). The obvious disadvantage of dynamic point models is that they do not consider space explicitly. This, however, has the advantage that their simulations are usually fast, require only small computer storage capacity and are able to simulate state variables in a highly detailed form.

**Dynamic area models** simulate larger areas in a single simulation. However, spatial heterogeneity is not taken into account, resulting in average representations of the properties of the area under consideration. In other models the state variables are structured with regard to essential properties, e.g., areas of stand age and stand volume (see matrix model EFISCEN, Nabuurs *et al.* 2000).

Advantages of dynamic models in general include that the temporal course of the state variables is interpretable. A major disadvantage of dynamic point and area models is that the simulations do not allow spatial interpretations of the results. In addition, highly resolved temporal input data for larger spatial scales may not be readily available.

**Dynamic regionalized** (distributed) models incorporate landscape heterogeneity by applying dynamic point or area models in parallel at many locations  $s_j$ , e.g., on a grid:

$\left(\frac{d}{dt} Y(t,s) = f(Y(t,s_j), X(t,s_j), \epsilon)\right)$ . Thus, this model type combines spatial and temporal aspects

of the landscape. However, the simulated locations are not spatially linked, i.e., do not communicate with each other. Applications of dynamic distributed models include e.g. the evaluation of global change phenomena such as predicting the behavior and properties of ecosystems at large scales under scenarios of possible future land use and climate. In the following, several examples of dynamic, distributed models are discussed.

An example of an *empirically derived forest model* is MASSIMO (Kaufmann 2001; Thürig *et al.* 2005). The model simulates the growth of individual trees at any of the sample plots of the Swiss National Forest Inventory on a 1.4\*1.4 km grid, under different forest management scenarios. Since the sample plots are very small (1ha) and thus not representative for the surrounding areas, the simulation results are lumped into geographical and ecological strata. An example of a *big-leaf-model* (Lexer 1995) is the biogeochemical model BIOME-BGC (Thornton 1998; Thornton *et al.* 2002). The model enables the calculation of fluxes and pools of carbon, water and nitrogen. These pools are extended over large areas; e.g., all leaves in a region form one "big leaf". In contrast to this coarse spatial and organizational resolution, BIOME-BGC includes relatively detailed processes of photosynthesis, nutrient and carbon re-allocation and partitioning, litter decomposition and a variety of mortality functions that allow realistic simulations of ecosystem properties over decades. *DGVMs* (Dynamic global vegetation models) (see comparison in Cramer *et al.* 2001) simulate the development of the vegetation composition across the whole globe, based on ecophysiological processes and nutrient cycling. Vegetation dynamics are based on annual net primary production and biomass growth; they include competition among plant functional types, disturbances and succession. *Frame-based models* (Starfield and Chapin 1996) simulate transitions between vegetation types ("frames") in grid cells on the regional to continental scale. The transition probabilities are based on intrinsic state variables and on rules that depend on environmental conditions. In some cases the transition probabilities are fitted to the results of gap models (Acevedo *et al.* 2001). This approach assumes biomes to be fixed entities, thereby neglecting the individualistic responses of species to changing environmental conditions (Davis 1986; Kittel *et al.* 2000). Finally, *patch models at many locations* have been applied to assess succession details in a larger spatial context, either explicitly on a geographical transect (e.g.

ForClim, Bugmann and Fischlin 1996) or in bioclimatic classes spanned by drought and day degree sum (Löffler and Lischke 2001). Advantages of dynamic large-scale models and of dynamic, distributed models include that the dynamic simulations can be interpreted spatially. The lack of spatial communication between the dynamic simulations on the discrete landscape elements is, however, a disadvantage.

### Dynamic, spatially linked spatio-temporal models (SLST models)

Introducing spatial communication in regionalized models leads to the group of dynamic, *spatially linked spatio-temporal* (SLST) models, the focus of this chapter. Landscape elements influence each other dynamically, not only locally, but also across larger spatial scales, revealing that local dynamics and spatial interactions are crucial in assessing landscape dynamics. Spatial interactions in natural systems and the models describing them occur at a variety of scales. On smaller spatial scales, interactions occur by flow of resources, e.g. water (Jakeman and Letcher 2003), or by competition for habitat or for resources, e.g., by lateral shading as in some individual-based, position-dependent forest models (e.g., SORTIE Pacala *et al.* 1993; Picard *et al.* 2001; SILVA Pretzsch 2002). On intermediate spatial scales, interactions may be represented by active movement or passive dispersal (Clark and Ji 1995; Neilson *et al.* 2005), of animals, plants, (e.g. by the formation of tillers) or (e.g., pathogens). Movement or dispersal determines the rate and direction of spread. For example, different seed dispersal mechanisms (e.g., ballistic, wind, animals) identify (together with generation time and a variety of other factors) a plant species' migration rate and direction. Variation in migration rates is one process that generates landscape heterogeneity.

Dynamic spatio-temporal models that account for such spatial interactions between locations  $z$  and the simulated location  $s$  (SLST models) take the form:

$$\frac{d}{dt} Y(t,s) = f(Y(t,z_i), X(t,s), \epsilon), i = \dots, n_s$$

Same as all dynamic models, SLST models include time in the temporal change of the state variables, either in discrete time steps (e.g., years, generations) or continuously. Spatial dependencies (and thus spatial interactions) in SLST models are coded by making  $f$  depend on a set of state variables  $Y(t,z_i)$  from the neighborhood  $i = \dots, n_s$ . The approaches to deal with these spatial interactions vary considerably (Caswell and Etter 1993). Classical, spatially implicit metapopulation models (Gilpin and Hanski 1991; Hanski 1999; Levins 1970) or network models (Green 1995) deal with subpopulations on patches or network-nodes without explicit positions. Distances are implicitly contained in transfer rates between the patches. In some position-dependent models (e.g., Pacala *et al.* 1993; Picard *et al.* 2001; Pretzsch 2002; Prevosto *et al.* 2003), explicit coordinates of the simulated biota are recorded. Other models simulate the state variables on each location in the simulation domain, either continuously (partial differential equation, reaction-diffusion, integral equation, integro-difference models, see Renshaw 1991), or in the cells or on the nodes of grids (coupled map-lattices Bjørnstad *et al.* 1999; Kaneko 1992). A specific type of lattice models are cellular automata (see case study 1 and Bolliger 2005; Bolliger *et al.* 2003; Syphard *et al.* 2005; With and King 1999; With *et al.* 2002). In cellular automata, each cell can take several discrete states (e.g. one single individual of different species) defined by rules that depend on the states of the surrounding cells.

Comparable to other ecological models, SLST models differ in their degree of complexity (generic/complex), in the organizational level (cells, individuals, biomes), in the relative importance of endogenous processes and exogenous drivers, and in the general model approach (deterministic vs. stochastic) (Bolliger *et al.* 2005).

## Applications of SLST models

SLST models are applied in various fields of landscape research where the processes and interactions that generate a landscape pattern are of interest. They are used to answer different types of research questions that can be subsumed under the following headings:

- Models to develop theories: What are the general mechanisms behind an observed landscape phenomenon?
- Generating and testing hypotheses: Why are landscapes as we observe them?
- Scenarios: What might happen, if... ?
- Projections: What might be in the future?
- Optimization and decision support for management: What is the best way to achieve a goal?

These questions are used in the following to give an overview of typical SLST model applications. Note that, although usually models are initially developed for certain applications, in many cases they can be attributed to several of these questions.

### **Models to develop theories: what are the general mechanisms behind an observed landscape phenomenon?**

SLST models are often applied to enhance the understanding of general mechanisms or laws that drive landscape processes and patterns. Certain observable phenomena in landscapes may be related to specific conditions and processes of one particular landscape, but may also be viewed as the result of general, even fundamental and universal mechanisms applicable to various independent systems. The search for universality or generality is fundamental to the development of ecological theory and is one of the most important aims of modeling studies (Green and Sadedin 2005; Jorgensen 1992). The models involved often belong to the group of SLST models and are usually parsimonious, i.e. simulate landscapes with very few generic and abstract variables and relationships.

The search for general phenomena in systems, including landscapes, often involves complex systems theory (Milne 1998; Strogatz 2001; Wu and Marceau 2002). One aspect of complex systems theory is self-organization. Self-organization originates from dynamic interactions between system constituents which spontaneously lead to order and organization in multi-component (complex) systems (Bak 1996; Perry 1995). A system self-organizes to a critical state (SOC) if its dynamics lead to a state characterized by scale invariance (Bak *et al.* 1987; Gisiger 2001; Solé and Manrubia 1995). Mathematically, scale invariance is expressed by power laws (straight lines on a log-log scale) (see also Bolliger *et al.* 2005), indicating that no particular scale (spatial, temporal) is singled out. This means in a spatial context that large-scale patterns may be predicted from small-scale patterns and vice versa. Scale invariance in a temporal context indicates that no particular time scale is singled out. The phenomenon of scale invariance has been observed in many research disciplines, including landscape ecology (Bolliger 2005; Bolliger *et al.* 2003; Cousens *et al.* 2004; Lennon *et al.* 2001; Milne 1998; Storch *et al.* 2002). However, empirical evidence for processes leading to scale invariance is still largely missing (Levin 1998) and the observation of power laws does not automatically imply that they have been produced by SOC (Allen *et al.* 2001; Li 2000a; b). However, it has been stated that scaling relationships may offer clues and hypotheses to how the fundamental processes of biology give rise to emergent diversity (Brown *et al.* 2002b). There is a wide range of modeling approaches to investigate complex systems, e.g., network models (Green 2000), partial differential equations with diffusion (Deutschman *et*

*al.* 1993), or coupled map lattices (Green and Sadedin 2005). An example of a parsimonious cellular automaton is presented in case study 1.

Other ecological theories where SLST models have played a crucial role include the concepts of patch-dynamics (Levin *et al.* 1993; Steele 1993). Population movements, e.g., the surprisingly fast migration of some plant species during the Holocene, have fascinated researchers since the 19<sup>th</sup> century (Reid 1899) and initiated a series of analytical spatially dynamic modeling approaches (reaction-diffusion, integro-difference, integral-equations). These are based on different hypotheses about the redistribution function for the propagules, e.g., Gaussian, negative-exponential, fat-tailed, (Clark 1998; Kot *et al.* 1996; Powell and Zimmermann 2004; Skellam 1951; van den Bosch *et al.* 1990). Another example for the contribution of spatially dynamic models to ecological theory are modeling studies of the survival and coexistence of species for understanding the effect of space on biodiversity and its maintenance (e.g. Chesson 2000; Gurney *et al.* 1998).

In contrast to the mostly parsimonious models used for general theories, SLST models tend to be more complex if applied to more specific questions of landscape research. Such specific questions are addressed in the next paragraphs.

### **Generating and testing hypotheses: why are landscapes as we observe them?**

One motivation for the application of SLST models is to understand observed pattern or development of a specific landscape to assess the relative importance of various exogenous and endogenous drivers. This requires analysis of past landscape dynamics, because the landscape state as observed in the present is the result of the landscape development in the past.

One topic for modeling such past landscape developments is the effect of disturbance history on landscape development. Coffin and Lauenroth (1989) used a gap-model to assess the effect of disturbances on grassland dynamics, and Wimberly (2002) investigated the influence of wildfire history on spatial forest composition using a combined forest-fire model. Wagner *et al.* (2006) used a cellular automaton for continuous tree growth combined with a lattice model for lichen (sub)population development and spread to explain abundance and genetic diversity of lichens in forest stands with different disturbance history. Moravie and Robert (2003) used a position dependent, individual based forest model to assess whether forest structure can be used to assess past forest dynamics, including disturbances.

The history of natural migrations is another area for the application of SLST models for the study of past landscape dynamics. Case study 2 illustrates the modeling of plant species migration during past climatic changes. Also the spread of herbivores and the resulting effect on plant distributions has been studied by SLST models (Lewis 1994; Maron and Harrison 1997; Pastor *et al.* 1999). A range of different models has been developed to study invasion of exotic plant species (see review in Higgins and Richardson 1996), including individual-based or lattice models (Higgins *et al.* 2000), cellular automata (Cannas *et al.* 2003), or reaction-diffusion models (Frappier *et al.* 2003).

The influence of heterogeneity on landscape or community patterns is for example studied with the individual-based, position-dependent forest model SORTIE that acts at small spatial scales (Pacala *et al.* 1996). Deutschman *et al.* (1999) found that the very fine scale light variability did not have any significant influence on the community structure. Land-cover change affected by biotic, abiotic and anthropogenic factors has been studied with semi-empirical frame-based type models (Brown *et al.* 2002a; Irwin and Geoghegan 2001).

### Scenarios: what might happen if ... ?

Once hypotheses about the mechanisms behind an observed landscape are generated and tested, models can be applied in an “if-then”-modus, evaluating either the model outputs’ sensitivity to different parameter or input variables, different forms of process functions or even different variants of model structure (sensitivity analysis). Alternatively scenario outcomes can be estimated with models whose control parameters’ or input variables are set according to a previously defined scenario (scenario studies).

A prominent application of SLST models in “what-if” studies is the unintended spatial spread of genetic information, either of genetically manipulated organisms or of resistant pests and weeds. Such complex systems require an integrated view of population dynamics, genetics, and physical transport processes. Different model approaches have been used to analyze this complexity, focusing on pollen dispersal (Baker and Preston 2003; Klein *et al.* 2003; Ma *et al.* 2004; Meagher *et al.* 2003; Tufto *et al.* 1997), population dynamics, and/or seed dispersal and genetics (Cresswell *et al.* 1995; Richter and Seppelt 2004; VanRaamsdonk and Schouten 1997). Pollen dispersal is taken into account either empirically (Baker and Preston 2003; Ma *et al.* 2004; Meagher *et al.* 2003) or by mechanistically describing pollen transport by wind (Loos *et al.* 2003; Tufto *et al.* 1997) or insect vectors (Cresswell *et al.* 1995). Also the effect of different types of landscape fragmentation on the persistence and migration of species has been studied with SLST models, e.g., with a single species spatial logistic model (Collingham and Huntley 2000), with a lattice model of plant functional types (Cousins *et al.* 2003), with a spatial gap model (Malanson and Cairns 1997), and with a model for the flight of individual butterflies in a structured landscape (Kindlmann *et al.* 2005).

### Projections: what might be in the future?

Probably the most tempting application of modeling is to develop scenarios for the outcome of changes (projections). The basic assumption behind projections is that all functional relationships that depend on time  $t$  whether directly or indirectly, e.g. by definition of rates and initial conditions, remain true. Furthermore, the intrinsic uncertainty, that might be acceptable at present, is assumed to be tolerable in the future.

One prominent field of SLST model projections is the ongoing and anticipated climate change. In this context it is crucial, whether species or ecosystems are resilient, adapt, or respond with diebacks to the changed environmental conditions, or can follow the climate change induced latitudinal and altitudinal shifts in the local site conditions (see e.g., Kirschbaum and Fischlin 1996). To study vegetation change and migration on the global scale, first steps are made towards including migration in dynamic global vegetation models (Neilson *et al.* 2005). On the continental to regional scale, various vegetation models have been extended to accommodate seed dispersal processes and have been applied in climate change studies: e.g., the frame-based model ALFRESCO (Rupp *et al.* 2000), the landscape model LANDIS (He *et al.* 1999), cellular automata (Iverson *et al.* 2004), lattice models (Dullinger *et al.* 2004), and forest and grassland-shrubland patch-models (Lexer *et al.* 2000; Peters 2002). Additionally, there is a wealth of models which study the combined effect of spatial-temporal fire dynamics, vegetation dynamics and succession, which are influenced by climate change (see classification in Keane *et al.* 2004).



### Optimization and decision support for management: what is the best way to achieve a goal?

An extension of “what-if” studies is the use of SLST models as tools for decision support in environmental management (Seppelt 2003). The aim is to facilitate decisions about whether intervention in environmental systems is desirable or likely to be necessary, or which interventions might yield the best results. This kind of application requires – besides the assumption that an extrapolation in time is correct – that the models used are robust regarding variation of the driving variables. In the decision-support mode SLST models can be applied in two ways:

**Scenario analysis:** SLST models compare the outcome of a given set of scenarios. Each scenario is a representation of a possible management strategy. As environmental processes are complex and highly interacting, scenario definition is itself a difficult task, requiring consensus within the group defining the scenario, e.g. consensus on the input variables of the model. Scenarios are frequently set up by discussing management options and future developments with a group of scientists, stakeholders and people involved in the process of interest (cf. Millennium Ecosystem Assessment 2005).

**Optimization:** Optimization procedures systematically search over all combinations of values of the input variables until given management goals are satisfied. Such procedures support consensus finding by providing transparent evaluations of scenarios. The major drawback is the high computational complexity that depends on two factors: the complexity of the process model (number of state variables, degree of nonlinearity etc.) and the spatial complexity (size of study area, grid cell size, number of spatially interacting processes). The more complex the simulation model and the larger the number of spatial relationships, the lower are the chances of success in the optimization. For such complex models, scenario analysis is usually the only feasible (Fig. 1 in Seppelt and Voinov 2003). Case study 3 gives an example for this kind of analysis.

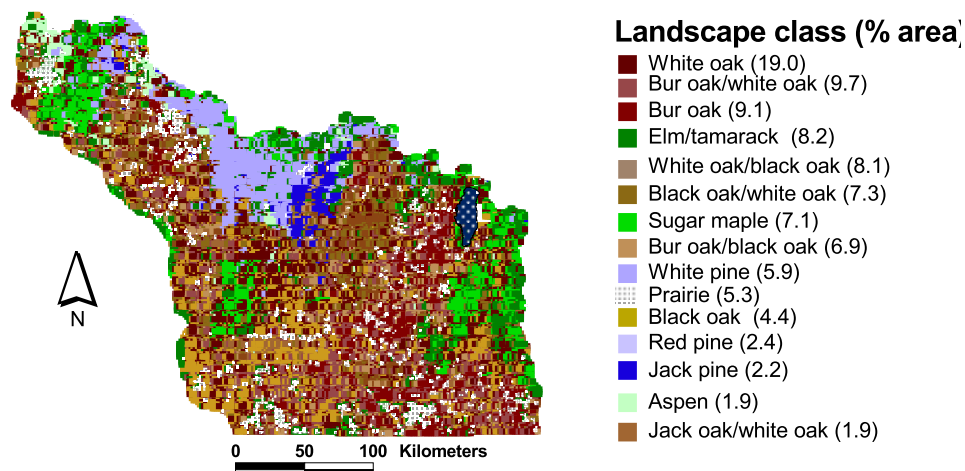


Fig. 1. Southern Wisconsin (U.S.A) represented by a quantitative (fuzzy) landscape classification.  $\phi=1.1$  indicates the degree of fuzziness with which the landscape was classified (for details see Bolliger 2005)

## Case studies

### Case study 1: assessing forest-landscape patterns using a cellular automaton model

This case study applies a generic cellular automaton model to statistically reproduce the spatio-temporal patterns of an empirical landscape. The model is generic with respect to the model structure. The model development rules define interaction distances for landscape patterns without accounting for any ecological detail. The interaction distances are identified by a circular radius  $r$  within which a cell on the landscape is chosen according to various stochastic rules (details cf. Bolliger 2005). The so chosen cell is then replaced by a randomly selected cell within a circular neighborhood of radius  $r$  ( $1 < r < 10$ ), where  $r$  represents the interaction distances. Small interaction distances are defined by  $r = 1$  encompassing 4 cells on the landscape. Intermediate interaction distances are represented by  $r = 3$ , accounting for 27 cells. Large interaction distances are identified by  $r = 10$ , encompassing 314 cells (details cf. Bolliger 2005; Bolliger *et al.* 2003; Sprott *et al.* 2002).

Input to the model is a historical landscape of southern Wisconsin (U.S.A). The landscape is represented by the US General Land Office Surveys, conducted during the 19<sup>th</sup> century, at a time prior to Euro-American settlement (Manies *et al.* 2001; Schulte and Mladenoff 2001; Schulte *et al.* 2002). Major landscape patterns (Fig. 1) are assessed using fuzzy classification (details cf. Bolliger 2005).

Comparisons between model simulations and the empirical landscape include temporal dynamics and spatial patterns. The temporal dynamics are assessed using cluster probability. Cluster probability is defined as the proportion of cells that are part of a cluster on the cell array. A cell is part of a cluster if its value is identical with the four nearest neighbors (e.g., bur oak). Cluster probability is thus a measure of aggregation of cells with identical properties and a measure to identify landscape patterns. The spatial development of landscape patterns is assessed using fractals (Bolliger 2005; Bolliger *et al.* 2003). Fractals provide measures to quantify spatial characteristics at a variety of scales based on algorithms that quantify the proportion of the geometrical space occupied by the fractal (Mandelbrot 1983; Milne 1988; 1991; Milne *et al.* 1992; Sprott *et al.* 2002).

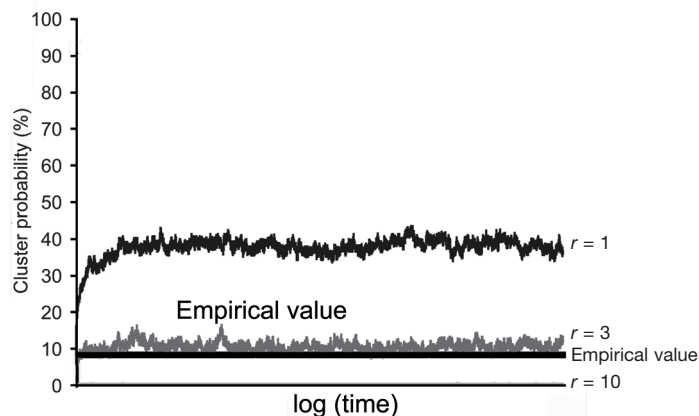


Fig. 2. Self-organizing landscapes: the simulated landscape self-organizes to the empirical value for intermediate neighborhoods for  $r = 3$  where  $r$  is the interaction distance (neighborhood) and the only parameter of the model. Cluster probability is defined as the proportion of cells that are part of a cluster on the cell array. A cell is part of a cluster if its value is identical with the four nearest neighbors (e.g., bur oak).

For the temporal development, large neighborhoods ( $r = 10$ ) result in simulated landscapes that do not self-organize (Fig. 2) as the likelihood that cells with identical properties interact is decreased. For small neighborhoods ( $r = 1$ ) over-organization is observed because landscape properties are more likely to be similar within small neighborhoods (spatial autocorrelation). If intermediate neighborhoods ( $r = 3$ ) are chosen, however, the model simulations self-organize to the respective empirical values. Interaction distances (connectivity) across the landscape are thus important to generate organized heterogeneity.

For the spatial development, the fractal dimensions  $D$  for both simulated and empirical landscapes are within comparable ranges for intermediate neighborhoods of  $r = 1$  and 3 (Fig. 3). Similarly, for the temporal development of neighborhoods of  $r = 1$  and 3 no particular

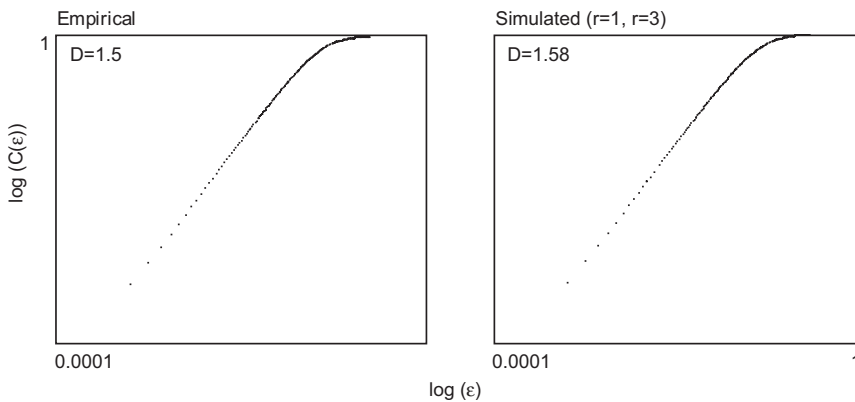


Fig. 3. Spatial characterization of model simulations: the fractal dimension  $D$  (slope of straight part of function) is similar for both the modeled ( $r=1$  and  $r=3$ ) and the empirical landscape. Scale invariance (power laws) are observed for  $r=1$  and  $r=3$ . Power laws indicate that no particular space scale is singled out.  $\varepsilon$ : distance.  $C(\varepsilon)$ : probability that two identical entities are distance  $\varepsilon$  apart.

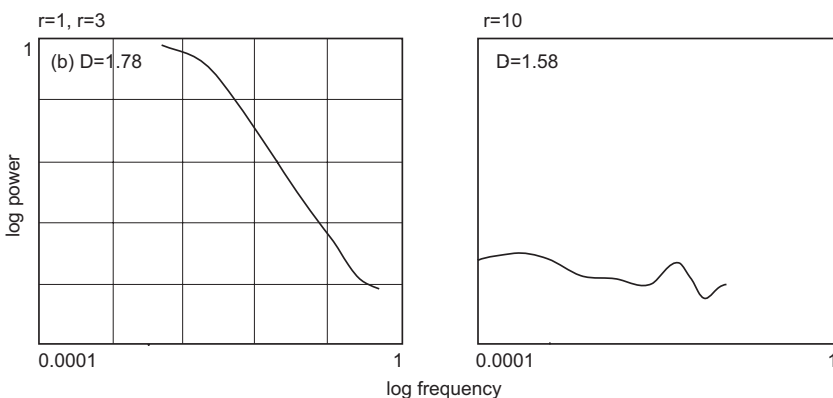


Fig. 4. Temporal characterization of model simulations: power laws are observed for simulations with  $r=1$  and  $r=3$ . Temporal scale invariance is observed, i.e. no particular time-scale is characteristic for the simulations for  $r=1$  and  $r=3$ . The neighborhood of  $r=10$  does not exhibit scale invariance since specific time scales are singled out and no straight line can be observed.

time-scale is characteristic for the simulations (Fig. 4). Thus, no particular space or time scales are singled out for small and intermediate neighborhoods, indicating that the patterns are self-similar and scale invariant with no characteristic scale length. Scale-free behavior reflects long-range correlations between space and time scales, indicating that processes may act similarly on landscapes across wide ranges of spatial and temporal scales.

Consistent with the empirical evidence, the simulated landscape shows self-organization and spatio-temporal scale invariance by relying exclusively on the internal variation of the patterns themselves since the model accounts for no ecological detail. It is therefore concluded that a generic model calibrated independently from specific ecological processes may suffice to statistically replicate a complex landscape. Other advantages of generic models include that simulations can be directly interpreted as a function of its few parameters, thus do not require detailed assessments of potential interactions with other model parameters. Limitations of the approach emerge from the fact that the simulated patterns are not spatially explicit since environmental constraints or gradients are not accounted for.

### Case study 2: simulating tree species spread with a migration model

To assess the potential of tree species adaptation to a changing climate, the SLST model TreeMig has been developed. It is suitable to simulate the succession and migration of tree species in a structured environment and under changing environmental conditions.

TreeMig (Fig. 5, Lischke *et al.* in press) is based on the distribution based, height structured population model DisCForM (see chapter upscaling, Lischke *et al.* 1998b; Löffler and Lischke 2001), in which the spatial within-stand variability is taken into account by theoretical distributions of tree densities and light intensities. To obtain the spatial model TreeMig, DisCForM has been implemented on a 1 km x 1 km grid. In each grid cell, trees in different height classes – tracked as population densities per height class and light availability class – germinate, grow, and die. TreeMig simulates explicitly seed production, seed dispersal to other grid cells, seed bank dynamics including density regulation and the development of seedlings/saplings.

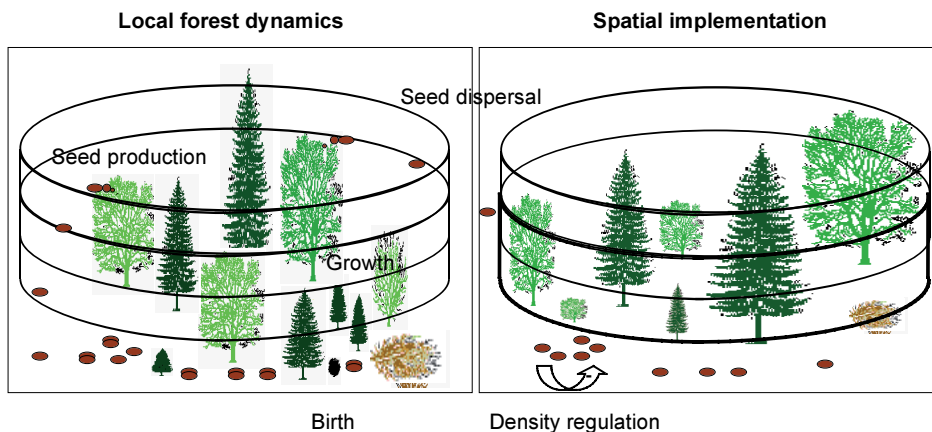


Fig. 5. Processes of the model TreeMig. The model is implemented on a grid. State variables are the densities of trees in different height classes. Trees germinate from the seed bank, grow, die and produce seeds. The seeds are dispersed to other grid cells, where they enter the seed bank. Seed bank dynamics follows a species-specific density regulation.

TreeMig was used to study the factors and processes driving the spatio-temporal vegetation development under past changing environmental conditions. The model was applied to the region of Valais (Switzerland) for the period since the last glacial during the Holocene (Lischke 2005). Figure 6 shows the spatial species composition at different time points

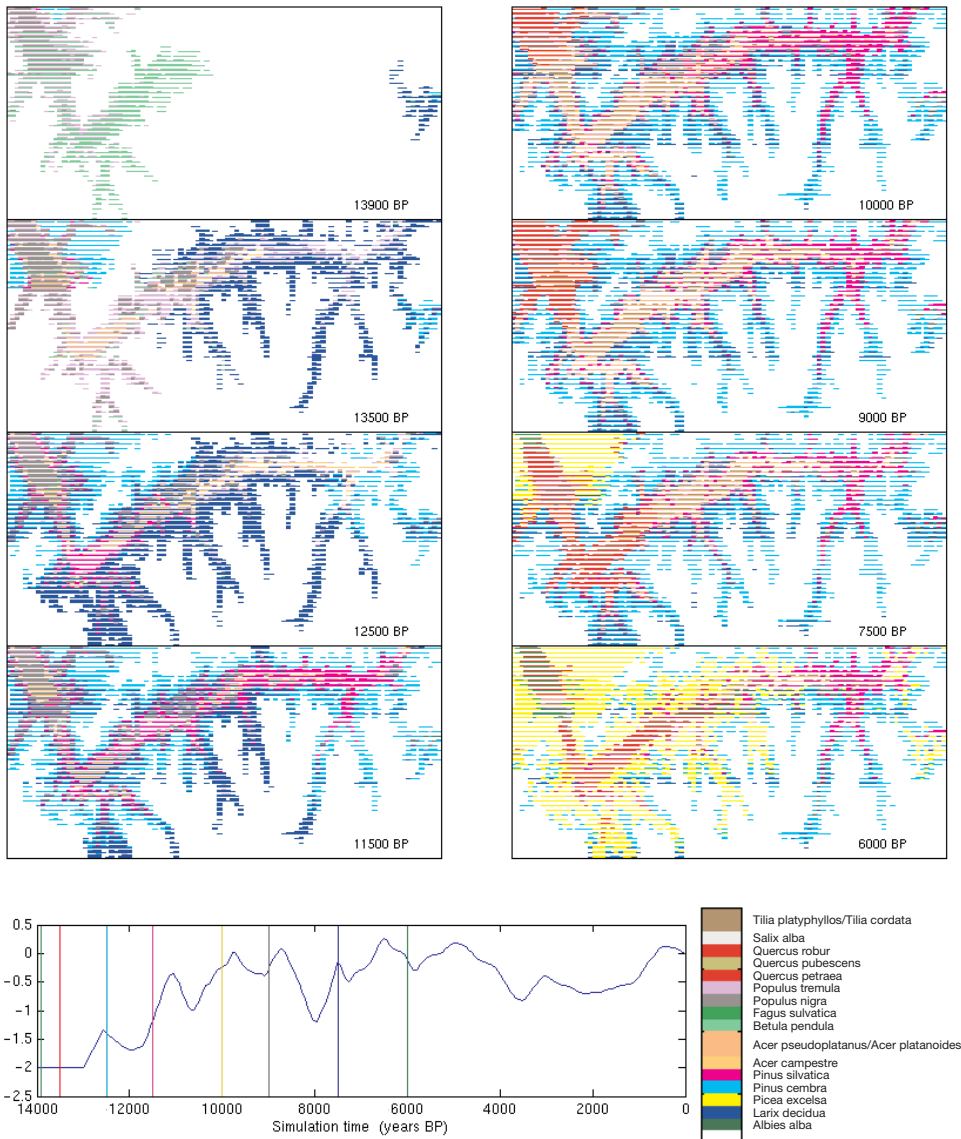


Fig. 6. TreeMig simulation of tree species spread on a 1 km x 1 km grid over 100 km x 50 km in the region of Valais, Switzerland. In each grid cell individual species biomass (t/ha) is drawn as a stacked column. A cell that is completely filled corresponds to 450 t/ha total biomass, resulting in white stripes in regions of low biomass. The graph at the bottom indicates the assumed temperature anomaly, the vertical lines refer to the times of the maps shown above.

during the simulation. The simulation is driven by time series of day degree sum, drought stress, and minimum winter temperature, based on a temperature anomaly scenario and current temperature and precipitation values. Years and sites of species immigration were derived from pollen records. The results show a vivid pattern of species spread, changes of dominance, and up and down shifts of the timberline. These phenomena are triggered by the variability of the external factors. Drastic changes of the boundary conditions, such as immigration of species into the simulation area or strong climate changes, initiate endogenous dynamics, i.e. migration and succession.

### Case study 3: using optimization for identification of landscape functions

Spatially explicit ecosystem models allow calculation of water and matter dynamics in a landscape as functions of spatial location of habitat structures and matter input. Seppelt and Voinov (2002; 2003) studied in a mainly agricultural region the nitrogen balance as a function of different land use and land cover schemes. The landscape model uses a grid structure to calculate water- and matter-dynamics in a spatially explicit way, e.g. flow of matter is calculated from cells to neighboring cells for surface, subsurface and groundwater according to the flow network and conductivities, to soil properties and land use. The task of the case study was to calculate optimum land use and fertilizer application for three different nested investigation areas, i.e. Partuxent watershed (2365 km<sup>2</sup>), Hunting Creek (77,8 km<sup>2</sup>) and a sub-watershed of Hunting Creek (20,5 km<sup>2</sup>), all in the Chesapeake Bay region, U.S.A (for details cf. Figure 12.1 in Seppelt 2003). Here, we focus on optimizing nitrogen loss out of the watershed; different aspects such as NPP or base flow are discussed in (Seppelt and Voinov 2003).

In a first step optimization tasks were formulated. This required the definition of performance criteria, which compare economic aspects, such as farmer's income from harvest "A", costs for fertilization "B", with ecological aspects, such as nutrient loss "C". As "A" and "B" can be quantified by monetary units and "C" is given for instance by mass per area, a weight  $\lambda$  (shadow price) is introduced in the performance criterion  $J$ , which is to be maximized:

$$J = A - B - \lambda C \quad (1)$$

These variables aggregate the processes of the entire study area. If  $J$  is defined for each grid cell ( $z_i$ ) separately, the optimization task can be simplified by

$$J(z_i) = A(z_i) - B(z_i) - \lambda C(z_i), \quad i = 1, n_{cells} \quad (2)$$

The maximum values of the criterion  $J$  have been calculated based on numerical optimization in spatially explicit dynamic ecosystem simulation models. Tests have been performed by Monte-Carlo simulations and gradient-free optimization procedures. The core idea of the investigation is to study optimum habitat patterns as a function of the unknown weight  $\lambda$  in Eqn. (1,2). Increasing means that nutrient loss out of the watershed is increasingly "punished" (compared to economic income by agriculture). Consequently the number of agricultural habitats decreases when  $\lambda$  is increased. The interesting results of these findings are i) although Eqn (1,2) describes a linear performance criterion, the resulting patterns are not linear, and ii) these nonlinear pattern are similar for all study areas of differing sizes, see Figure 7.

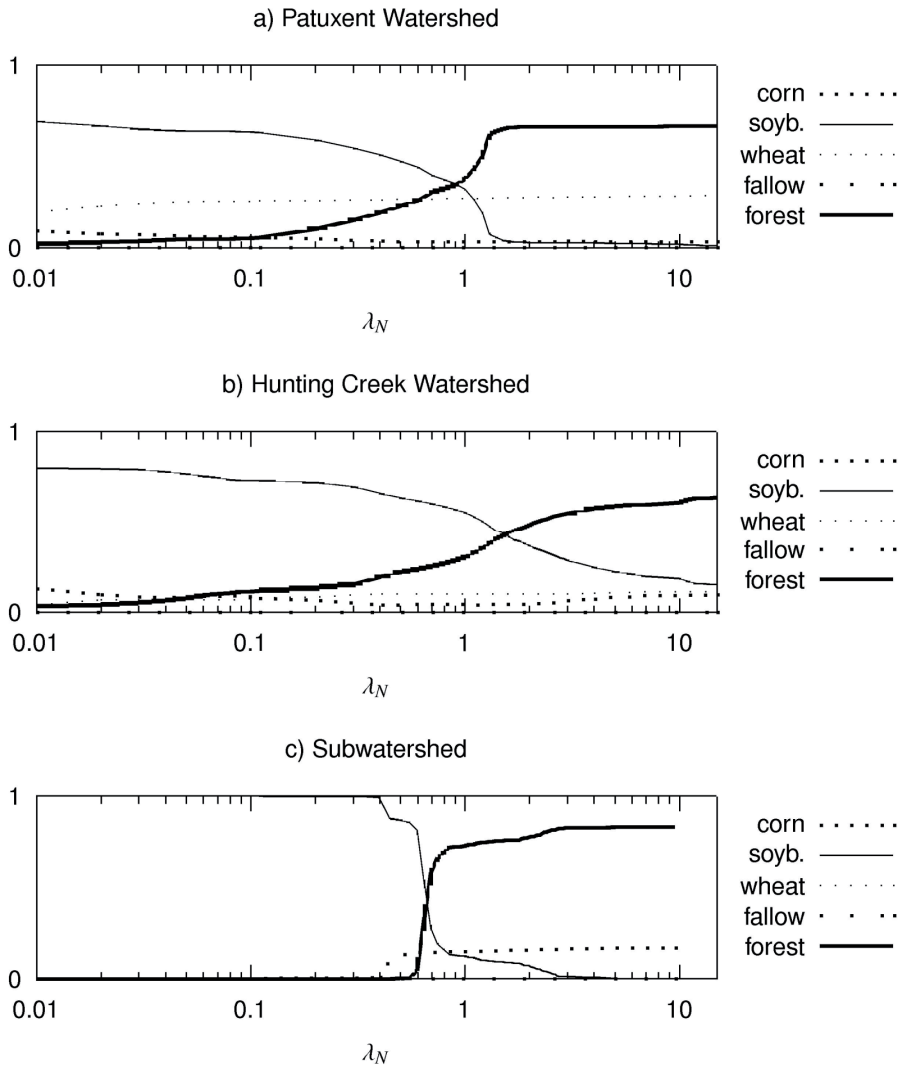


Fig. 7. Comparing optimum land use distribution patterns. In the present example yield is optimized against nutrient loss for three study areas, namely (a) Patuxent study area, (b) Hunting Creek watershed, and (c) the sub-watershed.

In addition to the aggregated results, one is interested in the spatially explicit results. Figure 8 displays optimum land use patterns for different  $\lambda$ -values. By doing so sensitive regions can be identified. For instance, the maps with higher values of  $\lambda$  show that forest habitat near the rivers and creeks supports retention capability of the ecosystem in terms of nutrients. As a result important areas with high retention capacity can be identified and fertilizer schemes can be evaluated depending on soil properties and topological relations to neighboring cells. The example shows that such optimization techniques can be a useful tool for a systematic analysis of management strategies.

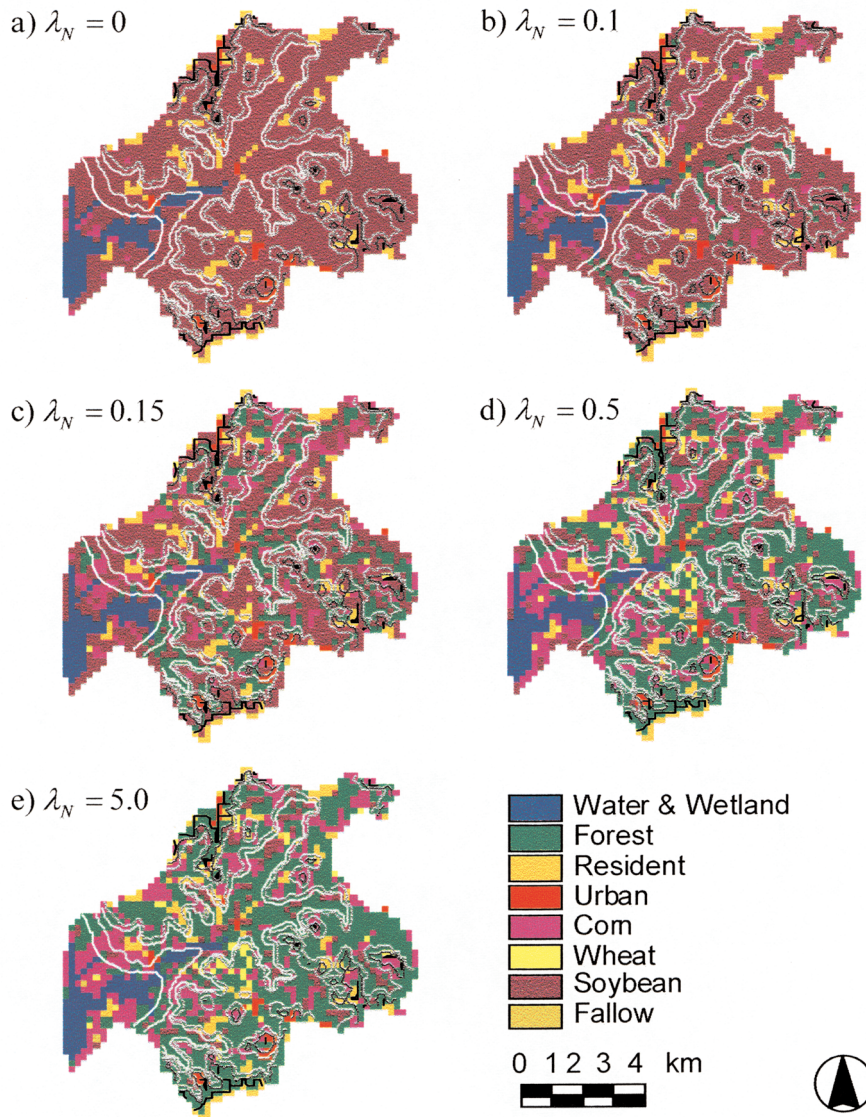


Fig. 8. Optimum land use maps derived from an SLST model. The models use different  $\lambda$  values (weights), namely  $\lambda=0$  (a),  $\lambda=0.1$  (b),  $\lambda=0.13$  (c),  $\lambda=0.5$  (d) and  $\lambda=5$  (e) (see text for more details). Lower areas near rivers and creeks can be identified by contour lines.



## Challenges

The presented applications have illustrated that SLST models are helpful tools for basic and applied landscape research as well as environmental management. However, there are major challenges involved in the development and application of SLST models, which include data availability, choice of appropriate model complexity and scale and model evaluation.

Modeling, simulation and testing model performance requires data and information on the processes of interest. A major challenge in landscape modeling is data availability. There is, on the one hand, a fast development in earth observation and monitoring technologies (esp. remote sensing), which support large-scale spatio-temporal modeling. On the other hand, a well-known experience in modeling studies is data scarcity: e.g., because modeling was not planned when a sampling strategy was developed and the data do not suit the modeling task or because they do not cover the spatial and temporal scale of interest.

Tests of models which are to be used to assess long-term consequences of environmental change are often hindered due to a lack of appropriate long-term data and there is clearly a lack of field experiments that run for more than 5–10 years. Alternatively, validation might be performed with historical archives, but has then to rely on data quality that never reaches the quality of recently measured data. For example, one important data source for testing simulations of vegetation change over long time periods are pollen assemblages. Yet, these are connected with a whole chain of uncertainties (Lischke *et al.* 1998a), concerning the interpretation of the pollen data, their temporal resolution and the input data scenarios required for such comparisons. Taking into account the above mentioned problems of model testing we recommend that (i) modelers should be integrated in field surveys from the very beginning and (ii) concerted actions for the collection of environmental data should be strongly encouraged (Jørgensen *et al.* 2000).

Another challenge is to find model approaches, whose complexity (in terms of number of state variables, parameters and processes) suits best the research question and the available data (Bolliger *et al.* 2005). Although this holds for ecological models in general, it is particularly true for SLST models, because the concept of interacting entities involves additional processes and parameters, and may produce a qualitatively new behavior. The aforementioned lack of appropriate information is one reason to adapt the model to the available information, which means to keep it simple (parsimonious). Such parsimonious models have the advantage that they are easy to manage and robust because they consist of only few highly aggregated and abstracted model components, i.e. state variables, process functions, parameters and driving variables. Sometimes they are even simple enough to be analyzed mathematically, e.g., by stability or bifurcation analysis. If the components of such a parsimonious model are chosen appropriately, it can be generic, i.e. can give insights into the general behavior of a landscape (see case study 2). However, generic models are usually not valid for a specific landscape or cannot represent specific landscape properties such as locations of landscape elements. Only if the model captures all essential basic processes, resulting in more complex models, projections or scenario studies of the specific landscape can be reliable. Complex models furthermore allow more detailed assessments of the spatio-temporal dynamics of landscapes and their drivers. However, due to the high number of parameters and potentially non-linear interactions, complex models can lose their robustness. Additionally, complex spatial models can require excessive computing time. Although this is only a technical constraint, it encumbers model development and testing and currently restricts applications either to small regions, coarse resolutions or very general formulation of the dynamics. Thus, the decision on which model complexity to choose relies on trade-offs between model generality, performance, accuracy, robustness, and manageability. Model complexity is partly associated with the scale at which the landscape dynamics is depicted.

Landscape processes operate and generate patterns across a range of hierarchical, spatial, and temporal scales. The choice of the adequate scale, the integration of model parts acting on different scales, and the change between scales are considerable challenges in landscape research in general. Scale changes of SLST models are even more complicated, due to the spatial interactions.

Modeling involves generalizations and thus introduction of uncertainties on a variety of levels. It is thus important that the model simulations are thoroughly tested for their robustness and validity (see Oreskes *et al.* (1994) for discussion on terms like “validation”, “verification” etc.) within the range of conditions in which they are to be applied. Furthermore, landscape models are often optimized for clearly defined study areas and for specific species that are simulated based on abiotic factors relevant for the study area. If they are to be applied under different conditions, validity needs to be tested for changing environments or a variety of situations (model generality). Due to the complexity of many landscape models it is evident that there is no standard procedure that provides appropriate tests. Rather, a variety of model aspects, e.g. model structure and behavior, can be evaluated using different approaches and scenarios. Model testing is often complicated by the lack of appropriate data. An alternative to comparing the models to empirical data is model comparisons, i.e. qualitative or quantitative comparisons within or between different model types.

## Outlook

Despite all these challenges, SLST landscape models will play an even more important role in future landscape ecology. Apart from the classical use in system understanding and scenario-testing, models will be increasingly used to interpret large-scale data (e.g., remote sensing signals), or for temporal and spatial interpolation of observations, e.g., in landscape inventories. Additionally, models will help to quantify state and trends of landscapes, and to identify critical thresholds where abrupt changes may occur. Thus, landscape models are and will be helpful tools for theoretical and applied research and environmental management, as they allow hypothesis testing for theory building and scenario testing for applications.

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