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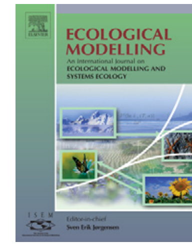

Analysis of pattern–process interactions based on landscape models—Overview, general concepts, and methodological issues

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ABSTRACT

Pattern–process analysis is one of the main threads in landscape ecological research. It aims at understanding the complex relationships between ecological processes and landscape patterns, identifying the underlying mechanisms and deriving valid predictions for scenarios of landscape change and its consequences. Today, various studies cope with these tasks through so called "landscape modelling" approaches. They integrate different aspects of heterogeneous and dynamic landscapes and model different driving forces, often using both statistical and process-oriented techniques. We identify two main approaches to deal with the analysis of pattern–process interactions: the first starts with pattern detection, pattern description and pattern analysis, the second with process description, simulation and pattern generation. Focussing on the interplay between these two approaches, landscape analysis and landscape modelling will improve our understanding of pattern–process interactions. The comparison of simulated and observed pattern is a prerequisite for both approaches. Therefore, we identify a set of quantitative, robust, and reproducible methods for the analysis of spatiotemporal patterns that is a starting point for a standard toolbox for ecologists as major future challenge and suggest necessary further methodological developments.

1. Introduction

1.1. System analysis and notations

Ecologists are interested in the interplay between environmental patterns and ecological processes. This is the pivotal clue to understanding ecological phenomena and complexity as a prerequisite for reliable predictions. The complex interactions of abiotic and biotic processes at different scales result in spatiotemporally heterogeneous and dynamic landscapes. The spatiotemporal pattern of exogenous environmental drivers sets the scene for interactions between individuals, populations, species and communities that themselves affect landscape patterns (Bolliger et al., 2005; Fortin and Dale, 2005; Wagner and Fortin, 2005). The analysis of pattern–process interactions at different temporal and spatial scales is one – if not the main – thread of landscape ecological research (O'Neill et al., 1986; Turner, 1989, 2005a; Turner et al., 2001; Wiens, 2002; Wu and Hobbs, 2002). It aims at (a) understanding the complex interactions between abiotic and biotic landscape elements and identifying the driving forces and underlying

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mechanisms as well as (b) at deriving reliable predictions for scenarios of landscape change and its consequences on, for instance, species conservation, biodiversity, and ecosystem functioning.

Environmental modelling is a broad field of research with a broad field of applications. Thus, the meaning of "*pattern*" and "*process*" may extremely vary between (sub) disciplines. However, we would like to present a general discussion leading to valuable generic statements and recommendations. We define *patterns* as observations that have a structure that is significantly different from a random process realisation. These patterns contain information on the mechanisms or processes which they emerge from (Grimm et al., 2005). Patterns have spatial and temporal aspects. The spatial aspect can for instance be the spatial distribution of individuals, species, resources, ecological functions or functional traits; but also the connectivity of habitat patches as well as the autocorrelation pattern of topographic, edaphic or ecological variables. The temporal aspect is illustrated by, e.g. changes in population sizes, the development of patch occupancy in a metapopulation, or a discharge variation together with the related concentration of pollutants or nutrients. Depending on the research question, both pattern aspects can be analysed separately or simultaneously. Frequently, scale and focus of a study determine, whether a certain phenomenon is interpreted as a pattern or a process. This becomes obvious in case of spatiotemporal patterns like patch occupancy patterns of metapopulations within dynamic landscapes or soil moisture and connectivity patterns in catchment hydrology.

Some striking patterns have drawn the attention of many researchers, e.g. vegetation pattern formation (Lefever and Tlidi, 1999), population cycles (Stenseth et al., 1998; Bjørnstad, 2000), synchrony of population fluctuations (Liebhold et al., 2004), mosaic cycles (Remmert, 1991) and shifting mosaics in woodlands (Olff et al., 1999) and grasslands (Watt, 1947; Fuhlendorf and Engle, 2004) as well as travelling waves (Kaitala and Ranta, 1998; Grenfell et al., 2001) or spiral waves in population dynamics (Hassell et al., 1991).

Processes are understood as the interactions of different objects in an environment. This can be, e.g. the movement of individuals in a landscape (Lischke et al., 2006b; Mildén et al., 2006; Price et al., 2006) or the transfer of water and nutrients in a watershed (Hattermann et al., 2006; Kokkonen et al., 2006), competition between species (Reineking et al., 2006; Tietjen and Huth, 2006), matter transport or the chemical reaction of a substance. On the one hand, processes depend on patterns, for instance, gradients in a landscape or the spatial distribution of barriers. On the other hand, they generate patterns. Depending on the object of interest and the system boundaries, processes may be characterised as exogenous like climate or fire or as endogenous, e.g. demography or species interactions (Bolliger et al., 2005).

1.2. Theories

Landscape ecological research is embedded in a history of theories that were developed in the last 20–30 years (Wu and Marceau, 2002). Hierarchy theory (O'Neill et al., 1986, 1989; Holling, 1992) was integrated with the concept of patch dynamics into the paradigm of hierarchical patch dynamics—explicitly incorporating heterogeneity and scale and integrating equilibrium, multiple-equilibrium, and non-equilibrium perspectives (Wu and Loucks, 1995). According to this framework, a landscape is characterised as a nested hierarchy of patch mosaics. Landscapes have also been referred to as complex adaptive systems (Levin, 1998). In contrast to traditional systems theory, this framework explicitly represents diversity, heterogeneity, and the role of adaptation (Hartvigsen et al., 1998). Further theoretical developments based on these frameworks deal with, e.g. invariant properties and processes creating scaling relations (Milne, 1998), self-organisation, self-organised criticality (Bak et al., 1988; Solé and Manrubia, 1996), ecological thresholds (Pascual and Guichard, 2005; Groffman et al., 2006), alternative stable states (Beisner et al., 2003; Scheffer and Carpenter, 2003) as well as the concept of resilience (Holling, 1973; Walker et al., 2004).

1.3. The role of models and simulations

Depending on the studied problem, the analysis of pattern–process interactions focuses more on the effect of pattern on processes (e.g. the effect of the spatial habitat configuration on colonization and extinction in a metapopulation, Mildén et al., 2006) or on the effect of processes on pattern (e.g. the effect of endogenous competition and resource distribution on community assembly, Reineking et al., 2006). Sometimes, the functional implications of both, patterns and processes, are analysed jointly, either in basic or in applied contexts (referring to ecosystem/landscape functioning or ecosystem/landscape services, cf. Turner, 2005a).

Due to the involved temporal and spatial scales, (landscape) modelling is the main tool for studying pattern–process interactions aiming at understanding and prediction. There are various landscape modelling approaches that can be categorised according to the underlying concepts or be related to different purposes (e.g. Bolliger et al., 2005, but see below).

There are different strategies to gain insights into the mechanisms underlying spatiotemporal patterns, e.g.:

(i) the direct approach of process description by mechanistic models and simulation (e.g. Hattermann et al., 2006; Lischke et al., 2006b; Mildén et al., 2006) and
(ii) the inverse approach inferring knowledge about environmental systems from data (e.g. Jeltsch et al., 1999; Reichstein et al., 2003; Cropper and Anderson, 2004).

While the first approach tries to explain patterns with processes through the study of simulated pattern realisations, the second tries to identify processes based on patterns by selecting models supposed to represent the underlying mechanisms and determining the model parameters.

Alternatively, this problem can be seen as being approached from two different starting points (Bolker, 2006):

(i) pattern detection and description, i.e. phenomenological models concentrating on observed patterns in the data, using functions and distributions having the right shape and being sufficiently flexible to match them, and

(ii) process description, i.e. mechanistic models concerned with the underlying processes, using functions and distributions based on theoretical expectations.

For both approaches, a large amount of elaborate methods has been developed in the last years in different disciplines. Both approaches require sophisticated methods of pattern description and quantification. Using ecological models as well as high performance hardware, more and more spatially explicit simulation models become available for the analysis of pattern–process interactions. This is a major step forward, as it supports landscape ecology with a methodological framework that enables a systematic, truly replicated analysis (Peck, 2004)—instead of in situ experiments. However, modelling itself is subjected to numerous constraints extensively discussed (e.g. Oreskes et al., 1994; Beven, 2002).

In this paper, we would like to promote progress for the theoretical and methodological developments in landscape ecology. Therefore, we synthesise the specific questions of pattern–process interactions presented in this special issue (and beyond) to identify some general core questions and to obtain some general recommendations for quantitative landscape ecology.

2. Core questions

Using the framework of model-based analysis of pattern–process interactions, different core questions can be identified:

(i) How can we identify, describe, analyse and quantify spatial and temporal patterns adequately?

(ii) How can we gain understanding of underlying processes through this kind of analysis? How can we infer a deeper understanding from pattern to process from single realisations?

(iii) As most patterns and processes are scale-dependent (Borcard et al., 2004; Keitt and Urban, 2005), how does the analysis deal with multiple scales?

These questions refer to a descriptive analysis of pattern–process interactions within a hierarchy of scales applying *phenomenological models*, which should be related to a conceptual model of the relationships between patterns and processes.

Based on this analysis or based on theoretical considerations new hypotheses can be generated and tested by experiments or by simulation (as virtual experiments, Wiegert, 1975; Winsberg, 2003; or numerical experiments, cf. Peck, 2004) in an iterative process to derive theory (Fortin and Dale, 2005). This step refers to *mechanistic models* that generate pattern realisations and leads to a second set of questions:

(iv) Do the general concepts of model development, application and testing focus on the topic of pattern–process interaction? Can we identify a general underlying philosophy and some general methodologies? And if yes, to which domain are these methodologies transferable?

3. Methodology of landscape analysis and landscape modelling—overview

We distinguish two different approaches to analyse pattern–process interactions. The first one starts with *pattern description* and *landscape analysis*, yielding the inverse problem of inference of underlying processes and parameter estimation. The second approach starts with *process description* and *landscape modelling*, yielding the direct problem of simulation and analysis of the resulting patterns.

3.1. *Landscape analysis: pattern identification, pattern analysis, pattern quantification, landscape pattern indicators*

3.1.1. *Overview*

The first step to understand and to manage the interplay between landscape patterns and ecological processes is the description and quantification of spatial and temporal pattern by means of phenomenological models.

Detection and quantitative description of spatiotemporal patterns in landscapes – landscape analysis – is performed by several approaches being developed in different disciplines. Some of them, e.g. time series analysis (for temporal patterns), Fourier and wavelet spectral analysis (for all kinds of patterns) as well as spatial and geo-statistics (for spatial patterns) have a strong statistical background. However, landscape metrics (Riitters et al., 1995; Gustafson, 1998; Li and Wu, 2004), which are very popular for quantifying spatial patterns, were developed in a landscape ecological context from – among others – information theory (O'Neill et al., 1988), fractal geometry (Krummel et al., 1987; Li, 2000) and percolation theory (Keitt et al., 1997).

Recently, there have been several attempts to compile these approaches and to provide some guidelines for selecting appropriate methods and supporting their every-day use in landscape ecological research (cf. among others: Special Issues *Écoscience* 9(2) and *Ecography* 25(5) published in 2002 as well as the recent Special Feature of *Ecological Applications* 16(1) published in 2006). Some comparatively new methods are presented that deserve a wider use in landscape ecology, for instance lacunarity analysis (Plotnick et al., 1993; Dale, 2000), (multi-)fractal models (Keitt, 2000) or spectral analysis (Lobo et al., 1998; Lundquist and Sommerfeld, 2002). All these approaches allow a multi-scale analysis of temporal and/or spatial patterns. Comparative studies recommend to analyse the data based on more than one method because different methods respond to different features in data (Dale, 2000; Saunders et al., 2005). Recent reviews list several needs coming along with the wider use of these methods (Turner, 2005a,b). They suggest that future research should concentrate on the integration of the plethora of landscape metrics and spatial statistics into an extended conceptual framework to understand spatial heterogeneity based on discrete and continuous representations and to account for the dynamics.

3.1.2. *Wavelet analysis*

An approach for time series and pattern analysis is currently gaining increasing attention in the ecological, geophysical and hydrological literature: wavelet analysis (Kumar and Foufoula-Georgiou, 1997; Torrence and Compo, 1998; Lark and Webster, 1999). Several authors use wavelet analysis for landscape pattern analysis: Bradshaw and Spies (1992) characterise forest gap structures applying wavelet analysis to transect data. Dale and Mah (1998), Dale and Powell (2001) as well as Rosenberg (2004) introduce wavelets for point pattern analysis in plant ecology. Brosofske et al. (1999) analyse diversity patterns on transect data and Redding et al. (2003) apply wavelets as an edge detection method to quantify the spatial patterns of soil temperature and soil moisture across forest edges. Similarly, Harper and Macdonald (2001) use this technique to analyse the spatial pattern of selected species along an edge-to-interior gradient. Su et al. (1999) calculate wavelet variances of maps with different spatial resolutions to study aggregation effects of land surface variables like albedo, temperature or NDVI and Csillag and Kabos (2002) present illustrative examples on how wavelet analysis can be employed for mapping two-dimensional landscape patterns. Grenfell et al. (2001) apply wavelet phase analysis to analyse spatiotemporal travelling waves of epidemics, Johnson et al. (2004) apply the same method to characterise spatial waves in larch budmoth outbreaks.

In recent examples, different studies use the so-called wavelet cross-spectrum of two variables. This is similar to cross-correlation (e.g. Bjørnstad et al., 1999, for analysis of population synchrony) or correlating spectra of variables by cross-spectral analysis (e.g. Pascual and Ellner, 2000; Price et al., 2006). Labat et al. (2005) apply cross wavelet analysis and wavelet coherence to hydrological time series, Jevrejeva et al. (2003), Maraun and Kurths (2004) as well as Grinsted et al. (2005) to geophysical time series. The latter two authors also provide software for this kind of analysis (http://www.agnld.uni-potsdam.de/∼maraun/wavelets/index.html for R; http://www.pol.ac.uk/home/research/waveletcoherence/ for MatLab). Maraun and Kurths (2004) present an instructive example highlighting potential pitfalls in the application of this method. Other studies in soil science apply these methods to spatial series, for instance to relate nitrous oxide emissions to soil properties (Lark et al., 2004), yield data to topographic indices (Si and Farrell, 2004) as well as saturated hydraulic properties to soil physical properties (Si and Zeleke, 2005). Applying a similar method, Jenouvrier et al. (2005a,b) relate seabird dynamics to climate dynamics and Klvana et al. (2004) show the link between solar cycle, local climate and porcupine dynamics.

3.1.3. *Habitat distribution modelling*

Another, comparably simple but well established methodology to infer underlying processes from snapshot pattern data is habitat distribution modelling (environmental niche modelling) that aims at understanding and predicting spatiotemporal distribution patterns (Guisan and Zimmermann, 2000). This is a phenomenological modelling approach, applying model-driven regression analysis (e.g. parametric generalised linear models, semi-parametric generalised additive models) as well as data-driven methods (e.g. non-parametric classification and regression trees). Here again, there are some recent Special Issues summarising the state of the art, i.e. *Ecological Modelling* 157(2–3), *Biodiversity and Conservation* 11(12) and UFZ-report 9/2004 (Dormann et al., 2004) together with a plethora of applications. The models relate species distribution data to environmental drivers in a hypothesis-testing framework. Implicitly, they assume equilibrium conditions, thus integrating conditions prevalent over longer time scales. The closer the relation between predictors and related processes, the deeper insight into the exogenous drivers controlling species distributions is possible (Guisan and Zimmermann, 2000). However, these predictors are merely proxies, and the analysis is not more than correlative and therefore potentially flawed by spurious correlations. Nevertheless, habitat distribution models yield valuable insights into important landscape ecological patterns and are a well-established tool in applications like conservation biology. They can be used to make predictions for spatial and/or temporal extrapolation (e.g. Schröder and Richter, 1999; Schadt et al., 2002; Guisan and Thuiller, 2005) allowing for scenario analysis (Theurillat and Guisan, 2001; Araújo et al., 2004; Rudner et al., 2007). Although predictions are usually good, habitat distribution modelling lacks of direct process implementation. But, since significant predictors are related to the underlying processes that are open for further testing by experiments or simulations (see below), habitat distribution models help to refine hypotheses of species–habitat relationships.

Nowadays, the underlying data sampling as well as the analysis are often carried out based on a multi-scale approach (e.g. Parody and Milne, 2004; Pearson et al., 2004; Graf et al., 2005; Morin et al., 2005). The main objective is then to understand the hierarchy of processes determining species' responses (Mackey and Lindenmayer, 2001). Keitt and Urban (2005) show another way to make scale-specific inference. They present a combination of regression and wavelet analysis using wavelet transformed predictor variables.

Recent developments in habitat modelling concentrate on

(i) spatial autocorrelation (Lichstein et al., 2002; Betts et al., 2006; Latimer et al., 2006),
(ii) multicollinearity of predictors (Mac Nally, 1996, 2002),
(iii) hierarchical modelling (Link et al., 2002; Thogmartin et al., 2004),
(iv) model selection (Johnson and Omland, 2004; Reineking and Schröder, 2006) and model averaging (Hoeting et al., 1999; Sanderson et al., 2005),
(v) model validation (Olden and Jackson, 2000; Reineking and Schröder, 2003), and
(vi) incorporation of expert opinion (Pearce et al., 2001; Lele and Allen, in press).

3.1.4. *The problem of single realisations*

The observed pattern depicts generally just one single realisation among several potential outcomes of process interactions (Fortin et al., 2003) because the studied processes do not have any true replication (replication in time would lead to an even more complicated analysis that has to deal with spatiotemporal issues and questions of spatial *and* temporal autocorrelation). So it is an important question how to infer underlying processes from pattern applying these sophisticated methods of pattern description. As Wagner and Fortin (2005) point out, inferring process from pattern is difficult, due to variation in the process(es) in space and time as well as due to the presence of additional confounding processes creating a mosaic of intermingled spatial patterns (cf. Poff, 1997; Fortin and Dale, 2005).

Again, there are several possible approaches: referring to habitat distribution models, resampling techniques, mimicking the sampling process like bootstrapping or cross-validation, are used for internal model validation (e.g. Olden and Jackson, 2000). If independent data are available, external validation is accomplished by model transfer (e.g. Dennis and Eales, 1999; Schröder and Richter, 1999; Binzenhöfer et al., 2005). Hierarchical partitioning can be applied to infer information regarding the effects of single predictor variables on the prediction (Mac Nally, 1996; Heikkinen et al., 2005).

Referring to neutral landscape models or null models (Gardner et al., 1987; Gardner and O'Neill, 1991; With and King, 1997), we may use stochastic spatial models to generate several spatial pattern realisations that can be compared to the observed pattern as shown by Fortin et al. (2003). Such an approach is applied by Remmel and Csillag (2003) to obtain confidence intervals for landscape metrics, which are necessary to decide whether patterns of several realisations differ. Their study is an important milestone for a better understanding of the statistical properties and behaviour of landscape metrics. Successively incorporating specific processes into these null models – or systematically and deliberately excluding them (Gotelli, 2001) – may yield insights into the underlying pattern–process interactions by applying still quite simple spatial models. This latter approach is just the opposite of the landscape simulation modelling approach, which considers lots of interacting processes to generate landscape patterns; this will be the topic of the following section.

3.2. *Spatially explicit landscape modelling and simulation*

3.2.1. *Models: pattern generators?*

The objective underlying a modelling and simulation exercise is to generate patterns that emerge under the assumption of a set of driving processes. Based on knowledge on the relevant processes of the considered system, one can set up simulation models using a plethora of methodologies (see Section 1). The Special Issue at hand as well as *Ecological Complexity* 2(2) published in 2005 shows many examples. These examples refer to different methodologies of how to implement process knowledge into a computer-based simulation environment. In general, these examples follow a direct and constructive concept of developing, designing and implementing a static or dynamic system that simulates spatial changes in a landscape.

What we do is something like estimating a set of state variables $\vec{Y}(t) = (Y_1, ..., Y_n)$ at time t which refer to a spatial unit s_i ($i = 1, \ldots, n$) that can be modelled as $\vec{Y}(t + \Delta t) = f(\vec{Y}(t), \vec{X}(t), \theta, \vec{\varepsilon}(t))$ where $\vec{Y}(t + \Delta t)$ depends on the recent state $\vec{Y}(t)$, environmental conditions $\vec{X}(t)$, disturbances $\vec{\varepsilon}(t)$ and model parameters θ (cf. Seppelt, 2003; Lischke et al., 2006a). Beven (2002) in his seminal, paradigmatic paper describes this kind of modelling as mapping landscape space to model space.

There is a variety of possible approaches for coding, specifying and describing processes within a model-based framework. An established categorisation distinguishes between mechanistic approaches using first principles from physics, chemistry or biology and phenomenological approaches using statistical or empirical relationships (Seppelt, 2003). According to Korzukhin et al. (1996) and Bolliger et al. (2000) this distinction is equivalent to the distinction between dynamic-transient and static-equilibrium approaches. Other dichotomies relate to bottom–up versus top–down approaches (Klemeš, 1983), which is equivalent to the distinction between exogenous and generic models in Bolliger et al. (2005). They can either be equation-based or rule-based, discrete or continuous in space and time, or deterministic or stochastic. All these dichotomies are only extremes on the respective gradients. Many of these differentiations are obsolete and only conductive to segregate different scientific communities but not to tackle urging research questions.

3.2.2. *Representation of space*

It is crucial to define the spatial scale and grain, i.e. what does s_i precisely denote. This could either be a representation of a landscape by a regular lattice, an identification of spatially quasi-homogenous, but geometrically irregular units (like e.g. patches in landscape ecology, MacArthur and Levins, 1964; Wiens, 1976; Roughgarden, 1977), hydrological response units/hydrotopes in hydrology (Kouwen et al., 1993; Becker and Braun, 1999), or erosional response units in geomorphology (Märker et al., 2001) or simply a discretisation obtained from the underlying numerics. This representation of space in the model determines the output as well as the parameterisation of landscape entering the model. The function $f(\ldots)$ hides three different and important interdependencies in the model:

(a) the dependencies of parameters and properties of the landscape element of interest,
(b) the interactions between landscape entities, e.g. the topology of interactions between landscape units, and
(c) the error-model assumed.

The first topic refers to the relation between the characteristics of a landscape element and the parameters of the process description, such as habitat suitability, soil properties or climate characteristics. Patterns mainly driven by these forces are called *exogenous*. The second refers to the specification of process interaction across landscape elements, such as overland flow of water or substances, competition or species movement. Patterns emerging from these internal interactions are called *endogenous* patterns.

3.2.3. *Recipes for defining f*

There is a variety of possible approaches that depend on the chosen concept of spatial discretisation. For instance, individual-based models (Grimm and Railsback, 2005; Reuter et al., 2005; Breckling et al., 2006) and pattern-oriented modelling (Grimm et al., 1996, 2005; Wiegand et al., 2003), rule-based or event-based systems in cellular-automaton models (Wolfram, 2002) as well as equation-based models (Roughgarden, 1998). Different models focus on different hierarchical levels, e.g. individuals (Parry et al., 2006; Tyre et al., 2006), populations (Price et al., 2006; Tyre et al., 2006), metapopulations (Hilker et al., 2006; Mildén et al., 2006), functional groups or communities (Lischke et al., 2006b; Reineking et al., 2006; Tietjen and Huth, 2006). They can incorporate different amounts of process knowledge (*white-box* models, i.e. physically based, derived from first principles versus *grey-box* models and *black-box* models, i.e. data-driven modelling). The application of $f(\ldots)$ either requires a well-known accepted set of equations and parameters for compiling f or to use inverse modelling to identify the structure of f and to estimate its parameters. The choice of the method should be guided not only by specific characteristics of the research question, but also by general considerations regarding explanatory value, transferability, and generality. These questions have been addressed from a philosophical point of view (Oreskes et al., 1994). Numerical measures of model performance using data-based physical model identification and quantitative indicators are available that take model residuals as well as model structure into account, for instance Akaike Information Criterion (Akaike, 1974; Burnham and Anderson, 2002).

3.2.4. *Model-based pattern analysis*

The core concept of model-based analysis of pattern–process interactions relates certain model parameters (or weighting or rules, θ in f) to spatiotemporal patterns. Thus, this can be interpreted as a pattern generator – either due to spatially distributed parameters or due to process interactions – which yields multiple representations of spatiotemporal patterns.

Under a direct approach hypotheses about underlying processes can be tested by running simulation models under different scenarios/parameter sets or with different model structures as virtual experiments and by assessing how well they reproduce observed pattern (e.g. Berger et al., 1999; Weiler and McDonnell, 2004; Grimm and Railsback, 2005). This strategy of rigorous experiments using strong inference (Platt, 1964) by contrasting alternative models or theories is one important advantage of simulation. It allows a systematic, truly replicated analysis (Parysow and Gertner, 1997; Peck, 2004; Grimm et al., 2005) and gives insight into parameter sensitivities and uncertainties (Hornberger and Spear, 1981; Beven and Binley, 1992; Wiegand et al., 2004).

3.2.5. *Inverse modelling*

The other way round, these models can be used in an inverse approach seeking for parameter sets that yield good predictions compared to observed data (Burnham and Anderson, 2002). Interestingly, there seems to be a convergent development of methods in ecological and hydrological modelling with respect to this approach. We think of inverse, pattern-oriented model calibration (Jeltsch et al., 1996, 1999; Wiegand et al., 1998, 2004) as well as generalised likelihood uncertainty estimation (GLUE, cf. Beven and Binley, 1992; Beven, 2006), both providing frameworks for model calibration, sensitivity analysis, and predictive uncertainty estimation. In the last years, GLUE has also found application in geomorphological modelling (Brazier et al., 2000) as well as in ecological modelling (Piñol et al., 2005) and other related fields like soil–vegetation–atmosphere transfer schemes (Franks and Beven, 1997). For complex simulation models exhibiting extreme runtime durations, Kennedy and O'Hagan (2001) present a promising approach of Bayesian calibration, sensitivity and uncertainty analysis that emulates simulation models (Kennedy et al., 2004, software available under http://marc-kennedy.staff.shef.ac.uk/code.html).

In inverse modelling, a set of performance measures is used to select among a large number of parameter sets (e.g. Hornberger and Spear, 1981). Alternatively, behavioural models are selected based on multiple patterns to be reproduced (e.g. Wagener et al., 2001; Holling and Allen, 2002; Rademacher et al., 2004). According to the underlying equifinality paradigm (Beven, 2002), there is no single "optimal model" but a set of multiple models providing similarly acceptable simulations. To reveal information about predictive uncertainty, these multiple models are averaged in a Bayesian manner, i.e. they are weighted according to their performance.

3.2.6. *Pattern comparison*

In such approaches, comparing simulated pattern to observed pattern is a crucial task to decide how well individual processes are represented (Grayson and Blöschl, 2000a). Moreover, the comparison can provide suggestions for changes in model structure and model parameters; discrepancies give information about how the models could be improved (Grayson and Blöschl, 2000b). Different performance criteria are used as pattern indicators to compare simulated patterns with observed patterns. Again, a variety of possible approaches exists, e.g. means and/or variances of some distributions of interest (or statistical relationships between both as in Tyre et al., 2006) or some other indicators, for e.g. community composition, vegetation cover, population sizes, mean plant age, root/shoot ratios, and species richness (as in Reineking et al., 2006).

Pattern comparison is also an important topic in model simplification, which is often a prerequisite to upscaling process-based models. In this Special Issue, the contributions of Hilker et al. (2006) as well as Tietjen and Huth (2006) deal with this topic. Whereas in the first study means and variances of some metapopulation parameters are compared between more or less complex metapopulation models, Tietjen and Huth (2006) compare times series of bole volumes resulting from different logging cycles in a tropical rain forest to show the equivalence between forest models with different complexity (and applicability).

In hydrological modelling, criteria for comparison of temporal patterns are far often simple goodness-of-fit criteria evaluating model performance in terms of model efficiency after Nash and Sutcliffe (1970), conventional objective functions like bias, root-mean-square error (RMSE), mean absolute percent error (MPE) or correlation coefficients. But, according to the GLUE-framework, likelihood measures of performance or fuzzy possibility measures (e.g. Aronica et al., 1998) should be preferred (Beven and Freer, 2001; cf. Hobbs and Hilborn, 2006, for the ecological context).

Regarding spatial patterns, there are some "classical" cell-by-cell-comparison methods like mean squared errors or Cohen's (1960) Kappa-statistic with modifications (see, e.g., Pontius, 2000; and accordingly Pontius et al., 2004). All these criteria ignore the spatial structure, so there is a certain need for improved methods for spatial pattern comparison (Grayson et al., 2002; Jetten et al., 2003). Therefore, Costanza (1989) developed a moving window approach to compare raster maps that has been extended by Kuhnert et al. (2005). Another approaches are presented by Shekhar et al. (2002) and Pontius and Cheuk (2006), who suggest some new measures for spatial accuracy evaluation.

In a study detecting processes that determine plant patterns, Jeltsch et al. (1999) use point pattern analysis to compare observed and simulated tree patterns in the southern Kalahari. Regarding spatiotemporal pattern, Parrott (2005) as well as Lischke (2005) apply a spatiotemporal application of entropy. Finally, Milne et al. (2005) use a wavelet transform to quantify the performance of models that predict the rate of emission of nitrous oxide from soil on different spatial scales.

3.3. *Interplay of landscape analysis and spatially explicit landscape modelling and simulation*

The preceding examples show that and how sophisticated methods for pattern identification and quantification can be applied to handle the task of pattern comparison (Jeltsch et al., 1999; Lischke, 2005; Milne et al., 2005; Parrott, 2005). As mentioned before, this is essential for rigorous experiments using strong inference as well as adaptive cycles of adaptive inference by contrasting alternative hypotheses (Holling and Allen, 2002).

Additionally, certain landscape simulation models need a proper discretisation to derive functional units for which local models are set up. This refers to boundary delineation and edge detection (Fortin, 1994; Fortin et al., 2000; Jacquez et al., 2000). We can cope with this task based on the same methods of spatial analysis mentioned above. As Csillag and Kabos (2002) show, wavelet analysis is suitable to delineate a parsimonious discretisation from multi-scale analysis. In the context of spatially explicit population modelling (and its application in conservation biological "population viability analysis", cf. Menges, 1990; Boyce, 1992), habitat distribution models can provide the spatiotemporal distribution of habitat patches (and habitat qualities, cf. Rudner et al., 2007; Schröder et al., submitted for publication) as functional units (Akçakaya et al., 1995; Söndgerath and Schröder, 2002; Larson et al., 2004).

Usually, phenomenological analyses provide a valuable complementary view and serve as preliminary surveys to generate hypotheses about underlying processes for experimental or simulation studies. The following studies on vegetation pattern formation may serve as illustrative examples: Rietkerk et al. (2000,2002b) present a geostatistical approach that results in a set of process-based models for different ecological systems, for instance semi-arid grazing systems (HilleRisLambers et al., 2001), arid ecosystems (Rietkerk et al., 2002a) or bogs (Rietkerk et al., 2004). These models lead to a more general understanding of this fascinating example of self-organisation in ecosystems (e.g. van de Koppel and Rietkerk, 2004).

4. Conclusions

There are several methods to identify, describe, analyse and quantify spatial and temporal patterns adequately and which, accordingly, support the quantitative study of pattern–process interactions in a multi-scale context. The different disciplinary origins of these methods highlight the importance of exchange of methods that has always been stimulating ecological research. Additionally, we presented a set of methods to infer from pattern to underlying processes; these methods include (among others) null models, virtual experiments by means of simulation, and inverse pattern oriented model calibration. Independent of the chosen approach, comparing simulated with observed patterns is a crucial task for all of them. Therefore, the identification of a set of quantitative, robust, and reproducible methods for the analysis of spatiotemporal patterns that can serve as a standard toolbox for ecologists represents a major future challenge for model-based analysis of pattern–process interactions. Spatiotemporal patterns include a large amount of information which is not yet exploited sufficiently for process description and landscape model testing. Thus, it is the interplay between phenomenological and mechanistic models, between pattern and process description that is promising for the improvement of our understanding of spatiotemporal ecological processes. Two main lines of development can be derived based on this review of methods and applications related to pattern–process interrelationships. First, process models need to include physical based parameters that assist understanding pattern emergence. These models then should be subjected to model simplification and aggregation but still maintain the physical foundation of its coefficients. Second, the use of inverse modelling to identify or specify processes that result in patterns which again are in accordance to observed patterns is a promising but computational intensive and methodologically still not elaborated branch on computational landscape ecology.

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