

Are Ecosystems Dynamical Systems?

Holger Lange

BITÖK, University of Bayreuth

D-95440 Bayreuth, Germany

Fax: xx49/921/55-5799

e-mail holger.lange@bitoek.uni-bayreuth.de

Internet: <http://www.bitoek.uni-bayreuth/Mitarbeiter/000125/en.html>

Abstract

The paradigm of dynamical systems as frame of description has been extremely successful for a variety of controlled systems. The ingredients of such an approach are an (assumed or known) *fixed* number of degrees of freedom, a phase space, state variables, and a (usually differential) equation of motion governing the temporal evolution of the system, or its movement in phase space along certain trajectories. Our focus of investigation are forest ecosystems. We will argue that they constitute a kind of system which does not belong to this class. The presence of memory effects and evolutionary processes demonstrate that the local history of these systems, embedded in an environment which is also partially created by them, is of utmost importance. There is no phase space for these systems. We therefore conjecture to characterize the system by its input-output mapping, considering it as a *filter*. Properties of this filter are quantified by *time series analysis tools*, identifying relevant time scales, correlations, periodicities, recurrences and other temporal structures. We show examples from hydrology and solution chemistry.

Keywords: ecosystems, time series, nonlinear methods, complexity

1 Introduction

Dynamical systems are *the* paradigm of almost all natural sciences. The possible behaviors of such systems can be grouped into three classes. The most simple systems show a regular deterministic behavior; small changes in the initial conditions lead to small changes in the trajectories, the phase space is finite dimensional. The second class are the deterministic chaotic systems; the exact computation of single trajectories requires infinite precise knowledge of the initial conditions. However, ensembles of trajectories may still be predictable in a statistical sense. The phase space is finite dimensional; if it is actually low dimensional, a number of methods may apply to characterize the chaotic behavior quantitatively. The third class are the stochastic

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systems with an infinite-dimensional phase space. Well-established methods exist to cope with such systems by *direct* modeling: numerical solution of the equations of motion, which are given (or assumed) a priori.

The experimentalist, however, faces the opposite problem: the data are given, there is no equation of motion of whatever class. Judging from measurements, the distinction between deterministic chaos and stochastic behavior is often elusive. A finite amount of data with an unknown noise level can easily lead to spurious results concerning (e.g.) the dimensionality of the attractor. (Hardenberg and Provenzale, 1997). The data requirements for a reliable calculation of the largest Lyapunov exponent, say, can be enormous and are in most cases not matched by the experimental time series. The ambitious goal to reconstruct the underlying equations of motion from the data alone has worked up to now for artificial (completely controlled) systems only, for similar reasons. Inverse modeling in this sense seems currently out of reach.

For our focus of attention, forest ecosystems, we will argue that the situation is even worse than that mentioned in the last paragraph. The crucial point is that in ecosystems, there is no fixed number of degrees of freedom. During evolution, generic *innovations* occur, leading to system variables simply not existent before, and *extinction* happens, the once-and-forever vanishing of variables (this has been called the “privileged” zero property (Kampis, 1991)). As there is no phase space for these systems, a partial differential equation approach is doomed to failure, as far as the whole ecosystem with all its parts (biological as well as abiotic) is concerned. Ecosystem theory has not come up with a single example of a successful reconstruction or prediction of both aspects for a given system. There are approaches to model the abiotic part explicitly - solving transport equations for matter and energy which are spatially distributed and notoriously overparametrized - and to model the biological part explicitly - population-biological models such as the Lotka-Volterra equation and its relatives, which notoriously ignore the important feedback of organisms onto their abiotic environment.

Whether this failure of process-oriented models for natural ecosystems is due to a lack of understanding of the relevant processes which will be overcome in the future or indicates a principal limitation is an open question. In cases where the biological situation is resetted from time to time via management interferences, as in agriculture and forestry, there exist empirical rules (e.g. yield tables) which work heuristically, but are unexplained from a scientific viewpoint.

We conjecture a paradigm shift from the “matter and energy” picture to an informational one (Hauhs and Lange, 1998). Environmental signals are processed by the system and transformed into output. Thus, the system is characterized by its input-output mapping; it is considered as a *filter* (Lange and Hauhs, 1994). Properties of this filter are quantified by time series analysis tools, identifying relevant time scales, correlations, periodicities, recurrences and other temporal structures. In this way, the information

content, the randomness and the complexity of input and output data sets are compared. A general tendency is a randomness reduction (smoothing) and a complexity increase (structuring) of signals on their way from the input boundary to the outlet of the system.

2 Ecosystems as Dynamical Systems

2.1 Biological and Abiotic Perspectives

The type of observer determines the perception of ecosystems. Traditionally, biologists concentrate on population aspects of the species to be found in a given geographical region, possibly delimited by natural boundaries (for migrating species). The abiotic environment serves as food supply and is otherwise structureless. There are only few approaches where e.g. the spatial resource distribution is explicitly taken into account (Rhodes and Odum, 1996). The boundaries perhaps relevant to the biota have no meaning for abiotic fluxes. Theoretical descriptions conceptualize populations as given by time-dependent densities, to which a differential equation approach applies. In the most simple cases (without any spatial structure), one constructs a set of coupled ordinary (nonlinear) predator-prey equations, with the Lotka-Volterra equations as prototypical example. Spatial spreading may be included in a diffusive manner (Murray, 1990); however, intra-species interactions as well as feedback to the environment is excluded in almost every PDE approach to population ecology. Long-term effects, predominantly ongoing evolution, is completely outside the realm of this approach. There is, e.g., no formal possibility to include the historical path of the system which led to its current state.

Complementary to that, a typical geophysicist or geochemist approach would be to concentrate on energy and matter fluxes across boundaries which are simply not existent for the inhabitants of the system. The latter are only relevant as sources or sinks of substances transported through and out of the system. A typical unit of study is the catchment (Moldan and Cerný, 1994). Thus, an ecosystem is considered as complicated chemo-physical factory or sophisticated thermodynamical machine. If such an assumption is a relevant abstraction, it should in principle be possible to investigate analytical tools from the theory of dynamical systems, which have been extremely successful in the past (may be this is an important reason for the appeal of the factory metaphor). Specifically, the transport processes are describable by appropriate nonlinear partial differential equations (like Richards equation and its relatives), and chemical reactions are described by sets of coupled algebraic equations. An obvious purely formal problem is the fixation of the appropriate number of initial and boundary conditions necessary to achieve unique solutions. In almost all field investigations, even the precise location of the boundaries is unknown, and the determination of the initial conditions (e.g. soil chemical or hydrological status) in such an extremely heterogeneous environment is elusive. In this situation, modellers rely on the assumption that the

system has a relatively short memory, rendering the precise structure of arbitrarily chosen initial conditions irrelevant at later times (prerun to equilibrate the system).

But this is only part of the story. The PDEs require the selection of spatially distributed parameter functions, like soil hydraulic conductivities or temperatures, which are only loosely restricted by measurements, due to the existing heterogeneity even on microscales. In practice, direct modelling, i.e. the fixation of parameter functions prior to simulation without fitting, is a rare exception. Rather, they are fitted to (part of) the data; as they are arbitrarily distributed continuous-valued function, severe overparametrization occurs. Consequently, with more than enough degrees of freedom, most of the data fits work quite well. The problem with the transport equations in ecology is that they are *too successful* to be informative. Little can be learned from the fitting exercise.

We hypothesize that a common source of these difficulties for both approaches is the neglect of historicity of the system. There are obviously long-term memory effects, the collection of (abundant) species at the location in consideration and also the structure of the abiotic environment is *not* arbitrary, but has a history. One cannot place a given ecosystem to another location and expect it to work also under the new conditions (this is sometimes called the "iron law of locus" in forestry). The shaping of the environment by the biota, their anticipative and adaptive behavior must be considered. Ecosystem managers (as opposed to scientists) know very well that, from a practical viewpoint, ecosystems can be maintained with moderate inferences for quite an extended period (centuries), with predictable yields, if the "iron law" is respected. This is not reflected in the dynamical systems approach, which has its dominant successes for highly controlled (thus highly artificial) conditions, mostly in the laboratory.

We therefore suggest to abandon the process-oriented approach for ecosystem description and substitute it by a data-oriented one. That is, considering the ecosystem (with catchments as prototypical examples) as functional unit which is described by the transformation they perform on their input to produce the observed output, one tries to characterize the type and details of the mapping, identify key variables and set limits to what can be learned about the systems interior from this outside perspective. This is not just a top-down approach, but also closely reflects the experimental situation of typical field investigations, making use of all types of information available from ecosystem monitoring programs.

In the next section, an example will be given where the process-oriented approach is much too successful to be useful even in a highly controlled situation.

2.2 An Explicit Example for the Process-Oriented Approach

One of the most common techniques to gain insight into transport characteristics (mean residence times, dominating flow paths) of natural catchments is the conduction of tracer experiments. We performed several such experiments for a very small (0.63 ha), spruce-covered catchment located in southwest Sweden (Lange et al., 1996, Lischeid et al., 1998). The catchment is completely covered by a roof, and natural precipitation is replaced by a sprinkler system. The catchment was held at hydrological steady state conditions to make the interpretation of transport parameters possibly unique and to exclude common excuses.

One of the experiments involved Deuterium as tracer, applied as a Dirac pulse. The observed breakthrough at the outlet was reconstructed with a relatively simple convection-dispersion model (Jury, 1982):

$$\frac{\partial c_m(z,t)}{\partial t} + \frac{1-\beta}{\beta} \frac{\partial c_{im}(z,t)}{\partial t} = D \frac{\partial^2 c_m(z,t)}{\partial z^2} - v \frac{\partial c_m(z,t)}{\partial z} \quad (1)$$

$$\frac{1-\beta}{\beta} \frac{\partial c_{im}(z,t)}{\partial t} = \alpha (c_m(z,t) - c_{im}(z,t))$$

where the soil is visualized as one-dimensional column containing mobile and immobile fractions of water; c_m and c_{im} are the tracer concentrations in the respective fractions, β is the ratio of water contents of the two fractions, D is the dispersion coefficient, v convection velocity and α is a transfer coefficient.

The breakthrough curve observed together with model reconstruction are shown in Fig. 1. Two of the parameters have been fitted and fixed, and only β and v are allowed to vary. Obviously, these *two* (!) degrees of freedom are already too much for a unique solution: the two drastically different parametrizations lead to undistinguishable reconstructions. Thus, the output from the system contains so little information that an identification of internal transport parameters is impossible. The tracer substance is not processed by the system in a way that would leave recognizable footprints, e.g. from the biota, or reveal higher dimensionality like transverse flow.

It seems obvious that the non-uniqueness or non-identifiability problems are much worse for complicated simulation models, solving e.g. three-dimensional transport equations for water, heat, and solutes under transient conditions. Calibration of these models are merely fitting exercises. On the other hand, the predictive power of this sort of ecosystem models is poor in many cases, for at least two different reasons. On one hand, the calibration to a specific data sets often renders the model inflexible; it loses its generalization capabilities ("overtraining"). It cannot "react" to input patterns never

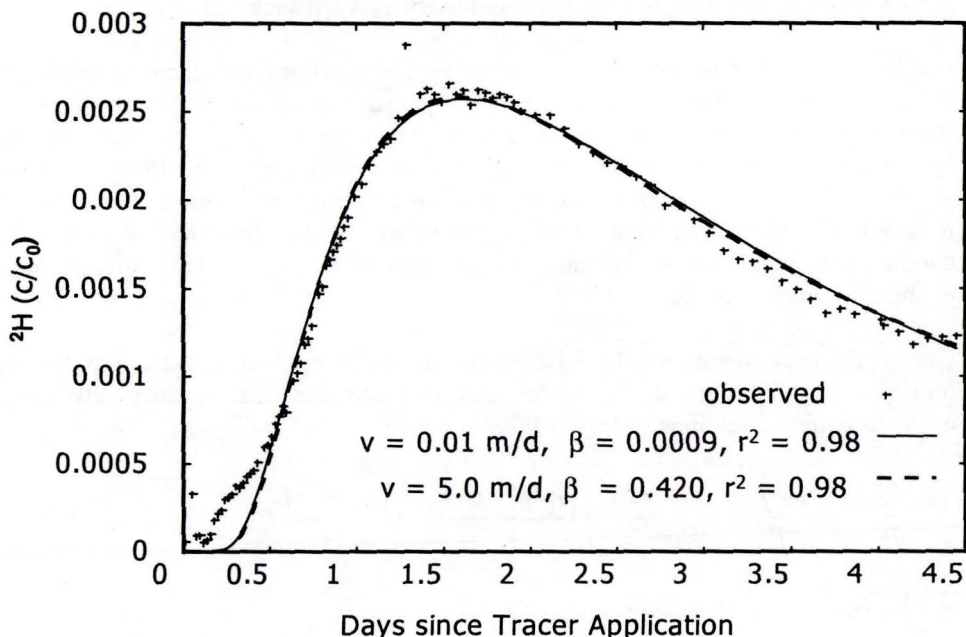


Figure 1: Breakthrough curve for a steady-state Deuterium tracer experiment, together with two different best fits with two parameters.

experienced before. On the other, there is clear evidence that there are limits in flux magnitudes below and above which the system does not process the signals properly or in the "usual" way. In hydrology, fluxes above the upper limit may appear as macropore flow (decoupled from the hydraulic potential) or even lead to catastrophic events (landslides). We are convinced that these so-called sensitivity limits should be incorporated in the formulation of an appropriate ecosystem theory (Hauhs and Lange, 1996).

3 Ecosystems as filters

The reconstruction of observed output fluxes from the observed input is *cum grano salis* easy, whereas internal information is either impossible to get (considering input-output relationships) or ambiguous (considering small scale measurements of arbitrarily heterogeneous local quantities). Consistent upscaling to ecosystem level is a major theoretical challenge (Wood et al., 1988).

It seems to be a consistent property of ecosystems with a well-defined output boundary (catchments in our case) that the spatiotemporal heterogeneity observed inside is not

reflected in the output. We have formalized this observation by hypothesizing that ecosystems act as *filters* (Hauhs and Lange, 1996). They transform random input into structured output, reducing the randomness. This should be reflected by calculation of appropriate randomness measures (cf. ch. 4.2). The output is also *redundant* to the input, as the over-success of curve fitting demonstrates. This is also confirmed by neural net simulations (Lischeid et al., 1998), where the input always contains enough structure to make the output learnable for the net. It is conceivable that this randomness (or information) reduction performed by the system is used for structure formation inside. In short, ecosystem act as information filters in their environment; the dampening and smoothing of signals makes the identification of internal structures impossible and unnecessary if one is interested in the functioning of the whole system as it is embedded in its abiotic environment.

4 The time series approach to ecosystems

4.1 Possible goals of a time series analysis

The arbitrariness of process-oriented approaches leads to the question how an effective characterization of ecosystem behavior with as few parameters as possible could be achieved. Our approach is by time series analysis of the input and output data. Our aim is not so much a detailed reconstruction of the output time series, but a characterisation of the mapping which the ecosystem performs, or to quantify the filter operation. This is accomplished by a detailed comparison of the same investigation methods for input and corresponding output fluxes; the most important example for our type of systems is precipitation as input and stream runoff as output. Possible goals include the identification of trends and periodicities, the quantification of information content, randomness and complexity of data, analysis of short- and long-range correlations and determination of the effective number of degrees of freedom. A possible implication is an answer to the question how complex a model of the data should be. It is obvious that spatially distributed highly parametrized models are not justified by the data, but a minimal number of parameters are surely required (the example in ch. 2.2 shows an extreme case). The complexity of models should be oriented by that minimal number. For its determination, principal component analysis or its nonlinear extension (Uhl et al. 1995) may be used.

4.2 Methods of investigation

We apply standard as well as non-standard techniques to selected data sets. Linear dependencies among variables are elucidated by calculating their *cross-correlation function*. The presence of periodicities and/or long-range correlations is exhibited by the calculation of *periodograms*. Possible instationarities, trends, extreme periods, periodicities and many other (nonlinear) features of the time series are visualized by *recurrence plots*. The phenomenon of high persistence is revealed by calculation of the

Hurst exponent, using the rescaled range statistics (Montanari et al., 1997). Concentrating on short-term structures and complexity considerations, we use symbolic dynamics to calculate two candidates for randomness and complexity, resp.: the *Mean information gain* (Wackerbauer et al., 1994) and the *Fluctuation complexity* (Bates and Shephard, 1993). A short technical description of the last two methods follows for the interested reader.

4.2.1 Calculation of Hurst exponents

Given the time series $X(t_i)$, we define partial sums

$$Y_n = \sum_{i=1}^n X(t_i) \quad (2)$$

and deviations from a linear increase of the partial sums within a given range or time scale k :

$$D(n,i,k) = Y_{n+i} - Y_n - \frac{i}{k}(Y_{n+k} - Y_n) \quad (3)$$

The range statistics then is

$$R(n,k) = \max_{0 \leq i \leq k} D(n,i,k) - \min_{0 \leq i \leq k} D(n,i,k) \quad (4)$$

The dependence of $R(n,k)$ from the (arbitrary) scale is factored out:

$$S(n,k) = \sqrt{\frac{1}{k} \sum_{i=n+1}^{n+k} (X(t_i) - \bar{X}(n,k))^2} \quad \text{with} \quad \bar{X}(n,k) = \frac{1}{k} \sum_{i=n+1}^{n+k} X(t_i) \quad (5)$$

such that our test statistics is

$$q(n,k) = R(n,k) / S(n,k) \quad (6)$$

This quantity is plotted versus k for various values of n (e.g. 20 different realizations), and the expected persistence behavior $q \propto k^H$ is fitted to the results.

4.2.2 Complexity measures

Their calculation is performed by first constructing a symbol string from the data X via *partitioning*:

$$\Sigma: X \rightarrow A, \quad x_i \rightarrow a_j \quad A = \{a_j\}, \quad j=0, \dots, A-1 \quad (7)$$

where A is the alphabet for the symbol sequence. In the examples presented, we have chosen a binary alphabet, and the partitioning was performed in a static manner: the

values of the observed quantities were cut at the median of their distribution, and all values below (above) the median were assigned the symbol 0 (1).

Then, one defines a word L length to group symbols together (in this article, $L=4$). The relative word frequencies p_i^L and conditional (or transition) probabilities p_{ij}^L are calculated. These are the ingredients to calculate the generalized Shannon entropy

$$H_L = -\sum_i p_i^L \log p_i^L \quad (8)$$

and our measure for randomness, the mean information gain

$$MIG_L = H_L - H_{L-1} \quad (9)$$

Finally, the fluctuation complexity (Bates and Shephard 1993) is given by (index L suppressed for simplicity)

$$\sigma_{fc}^2 = \sum_{i,j} p_{ij} \left(\log \frac{p_i}{p_j} \right)^2 \quad (10)$$

Analytical Results for Bernoulli sequences

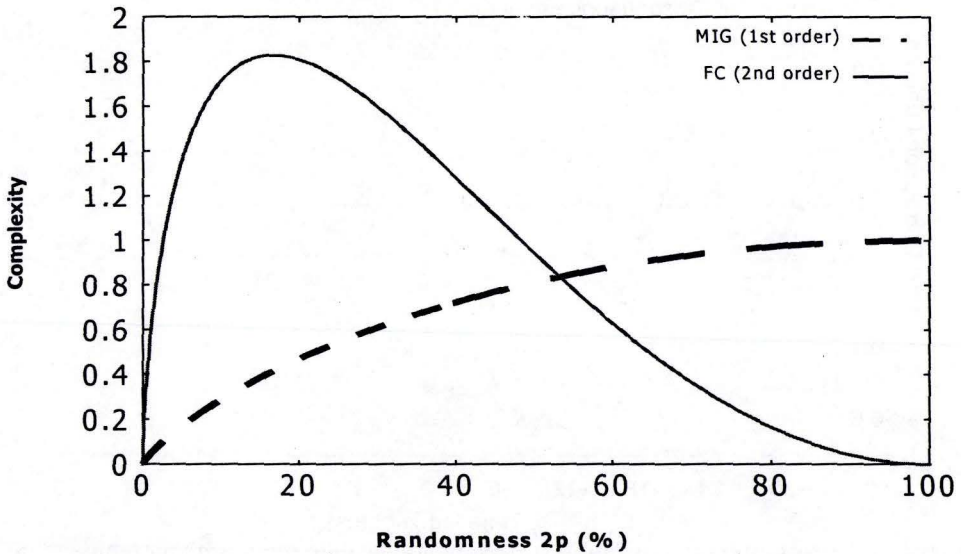


Figure 2: MIG and FC as a function of p for a binary Bernoulli sequence. First order quantities essentially measure randomness, second order ones have minima both at zero as well as maximal randomness and show a maximum at intermediate values.

The behavior of first and second order complexity measures, mean information gain (MIG) and fluctuation complexity (FC) in our case, is demonstrated in Fig. 2. Here, the probability of a simple Bernoulli binary sequence is varied as randomness parameter. The two measures can be calculated analytically in this case for infinite sequences. Whereas MIG is nonlinearly proportional to randomness, being more sensitive to structural changes in the region of low randomness, FC exhibits a maximum and vanishes for constant as well as completely random sequences. Thus, FC is closer to our intuition of what a "true" complexity measure should be.

5 Examples

5.1 Cross correlations

Figs. 3 and 4 show the linear dependence of three major ions in precipitation and runoff water from air temperature for the catchment Lange Bramke, Harz, Germany.

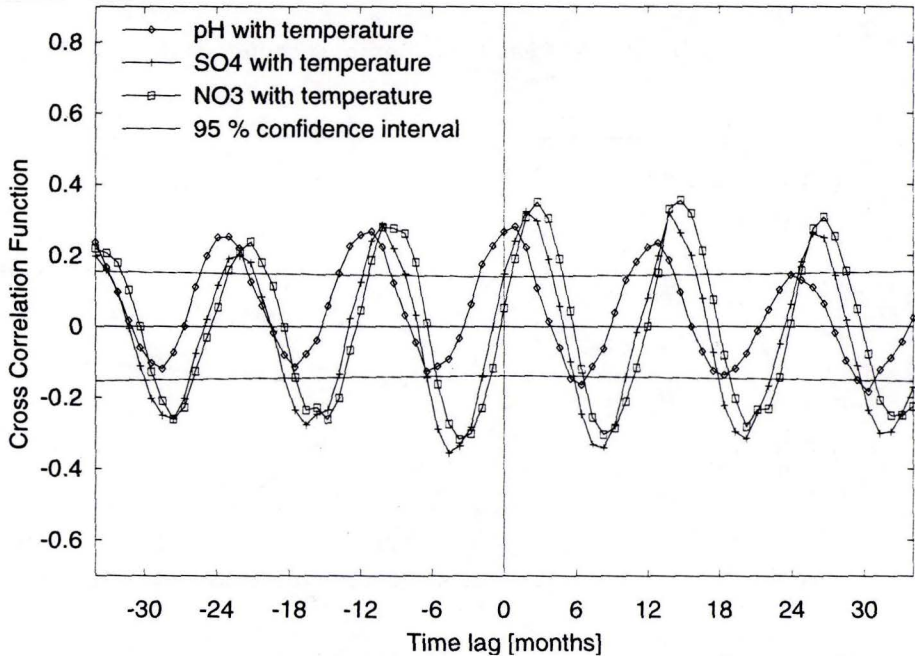


Figure 3: Cross correlation functions of precipitation solute series with air temperature.

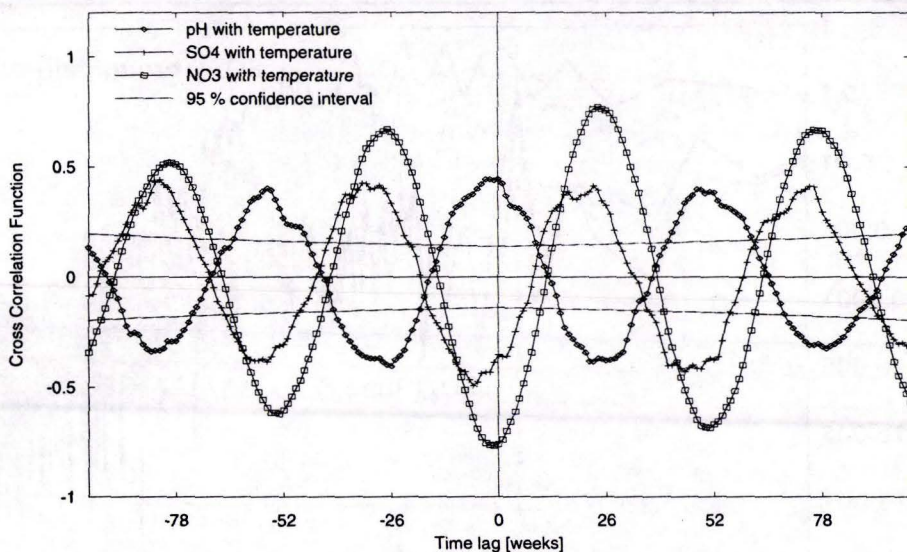


Figure 4: Cross correlation functions of runoff solute series with air temperature.

Besides the annual cycle, the input solutes are dominantly positively correlated around lag zero, although there are significant delays for SO_4 and NO_3 (temperature rises first). The transformation by the system changes the situation drastically: now, these two ions are *anticorrelated* with temperature around lag zero, demonstrating biological uptake and (in the case of NO_3) microbial activity in the system.

5.2 Periodograms

In Fig. 5, normalized power spectra of NO_3 and SO_4 from input (throughfall) and output (again from Lange Bramke) are compared. There are two main effects generated by the system: a yearly cycle is imposed, which is mainly a temperature effect, and at high frequencies, the power law behavior changes from $1/f^2$ to approximately $1/f$, indicating that now long-range correlations are present in the signals. These are due to memory effects such as microbial turnover of nitrogen or soil accumulation of sulfate.

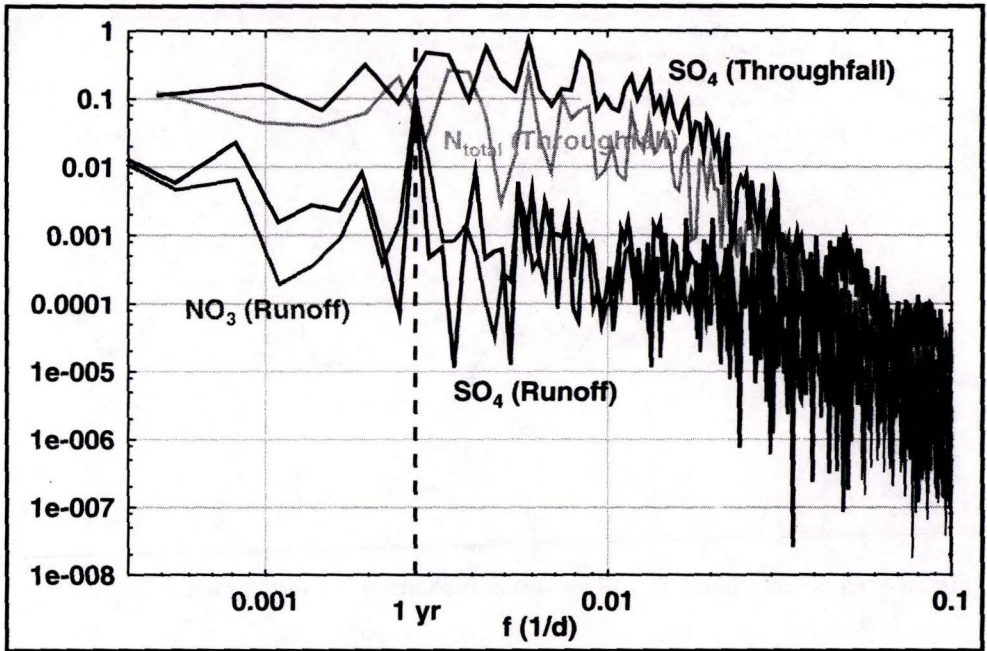


Figure 5: Power spectra for nitrate and sulfate solutes in precipitation and runoff.

5.3 Recurrence plots

Figs. 6 and 7 show two examples for recurrence plots of runoff signals from two different catchments located in Bavaria, Germany. Both plots span the same time period of 2.5 years¹. Dry periods are recognizable as regions with higher pixel densities. Periodic patterns appear as rectangles and are dominated by a yearly cycle. Although size, geology and climatic conditions are not too different for the two catchments, the visual impression of the two figures exhibits strikingly different behavior. The main difference is that one of the catchments (Lehstenbach) is completely covered by spruce trees, whereas the other has a mixture of beeches and oaks as dominant vegetation.

¹ For completeness, the technical details were as follows: embedding dimension two, threshold radius = 30% of the mean distance; delay one time step (daily values).

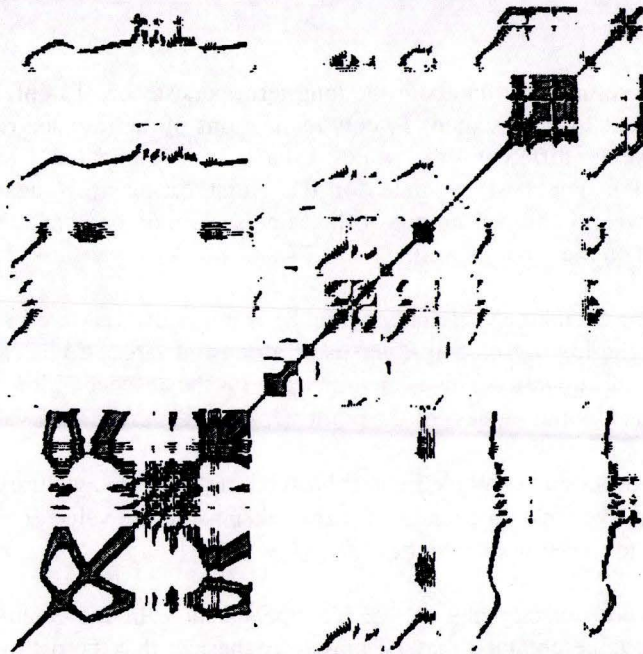


Figure 6: Recurrence plots for runoff from the Steinkreuz catchment.

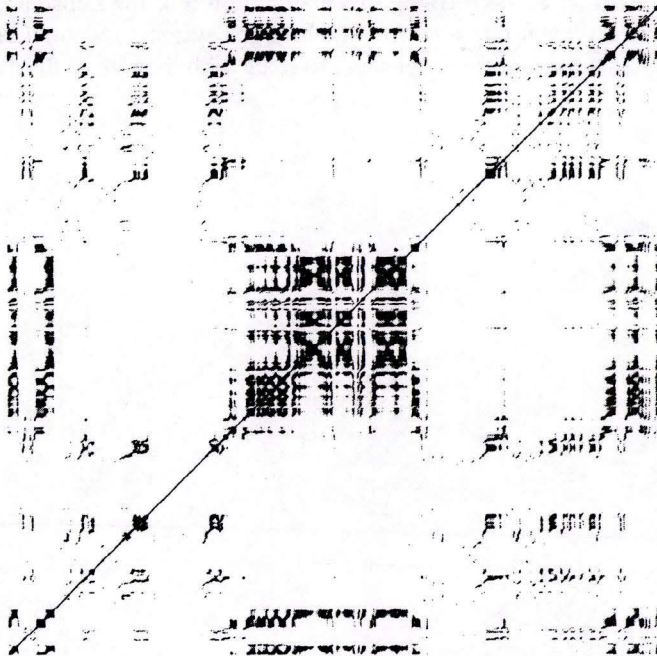


Figure 7: Recurrence plots for runoff from the Lehstenbach catchment.