

**Spatial ecology of peatland ecosystems:
Spatial self-organization and catastrophic shifts in bogs**

**Ruimtelijke ecologie van veen-ecosystemen – ruimtelijke zelforganisatie en
abrupte omslagen in hoogvenen**

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Summary

Positive feedback interactions, as between plants and their abiotic environment, may have the consequence that an ecosystem has alternate stable equilibrium states. As a result, a gradual change in environmental conditions may lead to discontinuous, catastrophic shifts in such ecosystems. Until now, the occurrence of catastrophic shifts is hardly predictable. However, a recently developed idea is that self-organized vegetation patterns might serve as an indicator for imminent catastrophic shifts. Because self-organized vegetation patterns are a common feature of northern peatland bogs, we examine to what extent these causally related concepts (positive feedbacks, alternate stable states, spatial self-organization and catastrophic shifts) might contribute to a better understanding of this type of ecosystems. Empirical and theoretical studies reveal that many positive feedbacks can be present in bogs, which may generate alternate stable states. Furthermore, stratigraphic peat analysis has shown that large and abrupt transitions do occur in bogs. However, the relative contribution of each of these feedbacks to the self-organized vegetation patterns in bogs and the possible relation with catastrophic shifts remain unclear. Conclusively, a research design is discussed that addresses the current gaps in knowledge about the way positive feedbacks may lead to alternate stable states and spatial self-organization in bogs, and its possible indication of catastrophic shifts.

Introduction

Positive feedbacks play a major role in the organization of ecosystems (DeAngelis & Post, 1991). Because of positive feedbacks within ecosystems, these systems may have alternate stable states (Scheffer & Carpenter, 2003), for example by positive feedbacks between plants and their abiotic environment (Rietkerk & Van de Koppel, 1997). The concept of alternate stable states was first proposed theoretically by Lewontin (1969), and is still an issue of considerable interest and debate (Bertness *et al.*, 2002). Alternate stable states mean that a system has more than one stable structure. Each stable structure has its own *basin of attraction*, meaning a range of ecosystem states that will develop towards this stable structure (Lewontin, 1969). Consequently, if such stable structure is reached, the ecosystems structure is resilient to perturbations within the basin of attraction. However, large enough perturbations force the ecosystem into another basin of attraction. Then, the system will be drawn towards another stable structure. This switch between basins of attraction is known as passing a catastrophic bifurcation (Kuznetsov, 1995; Scheffer & Carpenter, 2003).

Ecologists have long recognized that gradual changes in environmental conditions can cause abrupt changes in ecosystems (Carpenter, 1999). The passing of a catastrophic bifurcation can explain such “Big effects from small causes” (Ricker, 1963), resulting from an ecosystems property of alternate stable states (Holling, 1973). These “Big effects” are referred to as catastrophic shifts in ecosystem states, and several studies suggest that such shifts can occur in a large variety of different ecosystems (see Scheffer *et al.*, 2001 for a review). It is important to note that the term catastrophic refers to the nature of the change, not to the ecosystem development. The term can be a bit confusing, because sometimes the occurrence of a catastrophic shift is desired, and therefore stimulated (e.g. Meijer & Hosper, 1997).

Theoretical models (e.g. Rietkerk *et al.*, 1997) showed that the recovery from an undesired catastrophic shift is not achieved by restoring the environmental conditions that prevailed just before the shift took place because of hysteretic and irreversible dynamics. Restoring an ecosystem that has catastrophically degraded may therefore be very difficult or expensive (Carpenter, 2001), if it is possible at all. Therefore, it is desirable to know whether ecosystems are close to a catastrophic shift. Unfortunately, catastrophic shifts occur typically quite unannounced, and “early warning signals” of approaching catastrophic change are difficult to obtain (Scheffer *et al.*, 2001). Recent research on the other hand suggests that self-organized vegetation patterns are indicators for imminent catastrophic shifts (Rietkerk *et al.*, 2004b). If this is correct, the clearly visible self-organized vegetation patterns could serve well as “early warning signals”.



Figure 1: Pictures of regular spatial vegetation patterns from the Vasyugan Bog, Siberia (a,b, Courtesy Bleuten, Lapshina, Wassen) and from the Glacial Lake Agassiz, Minnesota (c, picture by B. Coffin, available on the World Wide Web on 7th Dec. 2004: <http://www.npwrc.usgs.gov/resource/1998/rlandscp/sub10-12.htm>)

Self-organised vegetation patchiness has been observed in the Vasyugan bog system in Siberia and in the Glacial Lake Agassiz complex in Minnesota, for example (Figure 1). These northern (boreal and subarctic) peatlands occupy less than 2% of the world's land surface yet contain about 30% of the global carbon pool (Gorham, 1991), and are located in the altitudes expected to undergo the greatest changes in temperature and precipitation in the next decades (Houghton *et al.*, 1995). Concern has risen that these peatlands may switch from sinks to sources of atmospheric carbon under a changing climate (Yu *et al.*, 2001). Therefore, it is interesting to test the above hypothesis for this kind of ecosystems.

In the following, each of these concepts (positive feedbacks, alternate stable states, spatial self-organisation and catastrophic shifts) will be addressed for bog ecosystems. Finally, a perspective is offered that addresses the current gaps in knowledge, and what future research is needed to permeate these gaps.

Positive feedbacks in bogs

Empirical results of Belyea & Clymo (2001) implicate that within a certain range of conditions, a positive feedback exists between acrotelm thickness and plant production. Nungesser (2003) argues that different *Sphagnum* species initiate differences in micro topography by facilitating their own environment. This positive feedback enhances initial topographical differences and leads to the formation of hummocks and hollows. Facilitation means that the *Sphagnum* species promote a high water table and also create acid and nutrient poor conditions that only very few species except *Sphagnum* can survive (Van Breemen, 1995; Van Breemen & Finzi, 1998; Gunnarson *et al.*, 2004). Moreover, *Sphagnum* reduces nutrient supply to vascular plants by intercepting deposited nutrients from the atmosphere (Heijmans *et al.*, 2002), which leaves only the mineralised nutrients as a possible resource for vascular plants. However, increased *Sphagnum* growth also limits this resource, because *Sphagnum* only produces relatively recalcitrant litter (Heijmans *et al.*, 2002). By shaping its environment in this manner, *Sphagnum* out competes vascular plants, thereby acting as effective ecological engineers (Jones *et al.*, 1994; Van Breemen, 1995). Hence, growth of *Sphagnum* positively feeds back to its own growth.

However, vascular plants also shape their own environment in a favourable manner, by increasing light interception because of overgrowing moss species (Heijmans *et al.*, 2002), covering the moss layer with their litter (Malmer *et al.*, 1994; Heijmans *et al.*, 2002) and creating drier conditions through increased transpiration (Van Breemen, 1995, Rietkerk *et al.*, 2004a). The latter mechanism might also drive another positive feedback interaction, namely a nutrient accumulation mechanism between vascular plant transpiration and convective nutrient transport (Rietkerk *et al.*, 2004a)

Alternate stable states in bogs

Several modelling studies suggest the occurrence of alternate stable states in bogs. In the bog model of Pastor *et al.* (2002), communities of moss monoculture, and communities where mosses coexist with vascular plants, are alternative equilibriums. The stability of either community then depends on nutrient input-output budgets and life-history characteristics of the species. The model of Logofet & Alexandrov (1988) describes the competition between trees and mosses as well as cycling of nutrients and organic matter. Their model results showed that forested bog and open raised bogs are both stable equilibriums, separated by an unstable equilibrium with intermediate vascular plant growth (Logofet & Alexandrov, 1988; Alexandrov & Logofet, 1994). The model of Hilbert *et al.* (2000) for a range of values of the water balance showed two stable equilibriums; bogs with a thicker acrotelm and lower water table, and bogs with

a thinner acrotelm and a higher water table. Also in the spatially explicit model of Rietkerk *et al.* (2004a), for a small range of parameter values, presence or absence of vascular plants are alternate stable states.

It can be concluded that different model approaches have led to the prediction that alternate stable states can occur in bogs. Although the model assumptions are mostly based on empirical data, direct evidence in the field for alternate stable states is still scarce.

Spatial self-organization in bogs

The spatial patterning in bogs is the result of the spatial interplay of densely vegetated elevated sites (hummocks or strings) and more sparsely vegetated lower sites (hollows or flarks). Vascular plants mostly grow on the hummocks while in the hollows Sphagnum mosses dominate. Regular spatial patterning of hummocks and hollows is commonly found in peatlands in North America and Eurasia (Sakaguchi, 1980; Belyea & Lancaster, 2002; Rietkerk *et al.*, 2004a), but the ultimate mechanisms underlying this widespread pattern are not well understood. However, the spatial patterning itself can provide a means for testing hypotheses about underlying mechanisms in the ecosystem, even though they cannot provide direct or complete evidence (Belyea & Lancaster, 2002). Most research has focused on the processes that lead to the so-called “string patterns” (Fig. 1c) on sloped substrate (e.g. Sakaguchi, 1980; Foster *et al.*, 1983; Swanson & Grigal, 1988). The string patterns consist of hummocks that have merged to linear ridges, perpendicular to the slope. The positive feedback between acrotelm thickness and plant production explained these string and flark patterns in the spatially explicit model of Swanson & Grigal (1988). However, these patterns can also be explained by the nutrient accumulation mechanism (Rietkerk *et al.*, 2004a), which can also account for the maze patterns (Fig. 1a,b) on flat ground. The maze pattern consists of densely vegetated bands of mostly vascular plants that grow in a more sparsely vegetated matrix where non-vascular species are predominant (Rietkerk *et al.*, 2004a). The recently reported maze patterns on flat substrate provide a new means to test which mechanisms account for the different spatial patterns.

Catastrophic shifts in bogs?

The “normal” course of raised mire ecosystem development is from pools towards climax stages as mire woodlands (Alexandrov & Logofet, 1994). This sequence of succession transitions is strongly correlated with the distance of the bog surface level to the water table. In pools the water is above bog surface level, in the climax stage the water level has dropped to approximately 50 centimeters below bog surface level (Alexandrov & Logofet, 1994). However, stratigraphic peat analysis has shown that in some cases pools replace climax vegetation (e.g. Walker & Walker, 1961). It is unlikely that submergence of the water table to this extent is caused by changes in climate only (Alexandrov & Logofet, 1994). Based on these kinds of observations, Frenzel (1983) proposed that small changes in external conditions might cause unexpectedly large consequences in ecosystems because regulatory processes had created an unstable equilibrium in these ecosystems. Also, peat core analyses have provided evidence for the occurrence of sudden changes in peat accumulation, which coincide with major vegetation changes (Belyea & Malmer, 2004). The nature of catastrophic shifts is in agreement with these descriptions.

The model results of Rietkerk *et al.* (2004a) suggest that under increased atmospheric N-deposition, areas where vascular plants are absent (moss monocultures) may shift catastrophically into areas wherein patterned growing vascular plants coexist with mosses, which is also in compliance with the model predictions of Pastor *et al.* (2002).

Perspectives

Theoretical and empirical studies of bog ecosystems give rise to the idea that the discussed concepts might improve our understanding of the functioning of these ecosystems. Although the hypotheses about spatial self-organization and catastrophic shifts in bog ecosystems have not been tested empirically yet, the dynamics of bogs as reconstructed from stratigraphic peat analysis show that catastrophic transitions could be an inherent feature of these ecosystems.

The pattern-oriented modelling approach (Grimm *et al.*, 1996) is useful for this study object. The objective of this approach is to understand the mechanisms that lie behind a pattern, and it can serve as a useful tool to formulate testable predictions (Grimm *et al.*, 1996). Most models discussed here take only one or few specific mechanisms into account, and investigate to what extent these mechanisms explain the observed patterns in nature. However, if the outcome of a model study shows that a mechanism explains a pattern, it does not mean that this mechanism drives the pattern formation in reality (Levin, 1992). Modelling these different mechanisms together allows one to make predictions about the relative contribution of each mechanism to pattern formation. Moreover, the interpretation of model outcomes benefits from focusing on multiple patterns (Grimm, 2004). For example, the model of Rietkerk *et al.* (2004a) also generates patterns of nutrient concentrations and acrotelm thickness. A closer study of such modelled effects of different feedback mechanisms will generate multiple independent hypotheses, which will benefit the interpretation of subsequent empirical findings (Belyea & Lancaster, 2002; Grimm, 2004). So a valuable step in future research would be to construct an integrated model that takes into account the discussed feedbacks, and investigate their relative importance in the functioning of bog ecosystems. Moreover, analysis of this model should focus on multiple patterns, in order to generate multiple independent hypotheses.

These hypotheses can then be tested through field measurements and experiments. As a result, the model performance can be optimised and calibrated. Subsequently model validation can be performed in a different study area.

Finally, this model can be used to predict the consequences of future changes in abiotic circumstances, as induced by global climate change for example. Through model simulations, predictions can be made how vegetation composition and thereby carbon fluxes may change in the near future. Moreover, it will be examined whether such changes are likely to encompass catastrophic properties.

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