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THESIS ABSTRACT

The complex adaptive character of spring fens as model ecosystems

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Abstract. Predicting the ecological effects of environmental perturbations remains challenging due to complex interactions between species and the environment, which constantly adapt the ecological memory and, thus, the future response of ecosystems. General theoretical frameworks like the Complex Adaptive Systems (CAS) theory might provide a solution. Here I discuss the applicability of the CAS theory for ecosystems by examining its three major principles (interaction, adaptation and scale dependence) for spring fens. For these ecosystems, adaptation of plant communities to historical environmental stressors (acidification) affecting the resilience to subsequent perturbations (climatic extremes) is empirically shown. Alternative stable states in community composition initiated by acidification turned out to be stabilized by abiotic-biotic feedbacks. Furthermore, ecological response of species to temperature showed high cross-scale similarity. I argue that the exceptional environmental character of spring fens qualifies these ecosystems as ideal model systems to test and further develop CAS theory for ecology and biogeography.

Keywords: biogeochemistry, crenic habitats, complexity, ecological memory, forest catchments, path dependence, positive feedbacks, scale dependence

Complex Adaptive System theory – towards a holistic perspective for ecology and biogeography

Understanding the processes that affect species distribution including the plurality of interactions among species as well as between species and the abiotic environment is one of the major challenges in ecology and biogeography (Likens 1992, Brown 1995). The integrative understanding of ecosystem functioning is nowadays a promising topic bearing in mind the past and ongoing human intervention. Furthermore, high uncertainty about future ecosystem responses is still characteristic for predictions of global change impacts and, thus, challenges ecological and biogeographic research.

A sound theoretical framework paired with empirical research is a prerequisite to increase our general understanding about ecosystem functioning and future responses. Integrative theoretical ideas of ecosystem functioning were already reflected in the theoretical considerations of Lotka (1925) and later taken up in systems ecology (Odum 1983) and in hierarchy theory (Allen and Starr 1982). All these classical systemic approaches in ecology considered self-organisation, interaction, and feedback loops between biotic and abiotic system elements as important properties of ecosystems. However, adaptation as a process emerging from all these properties (see Box 1) is mainly ignored by these classical approaches (Hartvigsen et al. 1998). Furthermore, the adaptive capacity of ecosystems is still understudied in ecological research and underrated in nature conservation and sustainable management, although it has been recognized as a major component of ecosystem resilience for several decades (Holling 1973, Gunderson and Holling 2002).

Complex Adaptive System (CAS) theory as a derivative of systems theory provides a general, integrative theoretical framework which explicitly accounts for the adaptive interactions between system elements and the environment (Hartvigsen et al. 1998, see Box 1). CAS theory promotes a combination of traditional community ecological and systems ecological perspectives, which is seen to be a promising way towards integrative ecological and biogeographic research (Brown 1995, Picket et al. 2007). Following the CAS theory, ecosystems can be defined as complex assemblages of biotic elements (i.e., populations of single species or communities) which adaptively interact with each other and with the abiotic environment, across a multitude of spatial, temporal and organisational scales (Levin 1992, Hartvigsen et al. 1998). Complex interaction, which means interaction characterised by feedbacks, is a major controlling factor for many ecosystems and is therefore seen as a major principle of CAS theory (Folke 2006).

Adaptation thereby includes any kind of physiological, behavioural, ecological and genetic response of organisms to unpredictable environmental changes (Holling 1973). While growing, species consume abiotic resources or actively transform abiotic environmental conditions and, thus, continuously modify the distribution of energy and matter in a given ecosystem with strong effects on the establishment and development of co-occurring species (Brown 1995). Thus, the structure and processes characterising ecosystems are strongly affected by the adaptive behaviour of ecosystems (see Box 1). Adaptation has therefore to be considered as a second major principle of complex adaptive systems (Folke 2006, Schweiger 2016). Adaptive behaviour of ecosystems is theoretically framed in the concepts of path-dependence (Holland 1992), ecological memory (Padisak 1992) and resilience (Holling 1973).

Characterised by complex adaptive interactions, ecosystems have to be referred to as historically grown systems (Margalef 1975, Anand et al. 2010) a fact of major relevance for biogeographic

Box 1: Definitions of concepts and terms used in the framework of Complex Adaptive System theory.

Adaptation: Here adaptation is defined as a continuous adjustment in the reaction and attributes of an ecological system as a response to changing environmental conditions (Filotas et al. 2014). In other words, adaptation is the evolving property of complex systems, which results from continuous interactions and feedbacks among biotic elements (e.g., species) as well as between biotic elements and abiotic environmental conditions (e.g., soil nutrients) which affects future interactions and feedbacks (Holland 1992, Gell-Mann 1994, Holland 2006). Adaptation therefore describes system evolution including system learning by forming an ecosystem memory (Holland 1992, Gell-Mann 1994, Power et al. 2015).

Complexity: Interactions characterised by feedbacks, thus the interconnectedness, of elements in a system. Due to the plethora of interconnections which characterise complex systems, they cannot be sufficiently described by the properties of their individual elements, making a complex adaptive system more than the sum of its parts. The interaction of individual elements thereby results in the emergence of system structures (e.g., food webs) and the flux of energy, matter and information on multiple scales which in turn might affect subsequent interactions among the system elements (Levin 1998).

Complex adaptive systems (CAS): Here, CAS are defined as a collectivity of adaptively interacting elements. Thus, diversity, individuality and organization of biotic elements (e.g., species), interactions among these elements and between the elements and the abiotic environment across scales, non-linearity and stability in the system’s reaction to environmental perturbations and the dependency of these reactions on previous circumstances (path dependence) play a major role in complex adaptive systems (Gell-Mann 1994, Levin 1998, Schweiger 2016).

research which focuses on the effects of ecological and eco-evolutionary history on current biogeographic patterns. How a certain ecological system reacts to environmental perturbation strongly depends on the past and present environmental circumstances as well as on the intensity of internal interactions between the system elements (Gell-Mann 1994). The present state of an ecosystem can therefore evolve in several possible future states depending on the system's history, the extent of species interactions and the current environmental setting (Power et al. 2015). Thus, sound assessments of future system trajectories critical in global change impact research have to account for the system's memory in combination with the current context of environmental changes (Power et al. 2015, Schweiger et al. 2015a).

Scale dependence of processes and patterns is another property emerging as a consequence of complex interactions and should be considered as an additional, major principle characterising complex adaptive systems (Schweiger 2016). The complex adaptive character of ecosystems causes strong links between processes and observable patterns acting on different spatial, temporal and organisational scales (Hartvigsen et al. 1998). Consequently, the scale dependence of processes and patterns has become an active research field in ecology and biogeography (Margalef 1975, Hartvigsen et al. 1998, Sandel 2015). However, scale dependence is often seen as a sheer matter of fact which researchers have to bear in mind instead of a research topic itself. Asking the question about the underlying drivers of scale dependence in ecological systems might therefore help to increase our mechanistic understanding about cross-scale interactions (Sandel 2015, Schweiger and Beierkuhnlein 2016) and resilience (Folke 2006) of ecological systems.

Although system adaptation causing ecological memory as well as scale dependence are two long-standing major topics of biogeographic research, a framework combining these two aspects in an integrative theoretical concept is missing. I therefore suggest to treat these usually separately considered ecological properties as integrative parts emerging from complex interactions by referring to the CAS theory as a sound but, in the biogeographic literature, mainly unknown conceptual framework. I thereby will specifically focus on (1) how complex interactions among species and between species and the abiotic environment change the structure and response characteristics of ecosystems to environmental perturbations through time, and (2) the importance of abiotic cross-scale relations on the scale dependence of species responses to environmental changes.

Spring fens as models to test the CAS framework

Model ecosystems allow studying single parts of an ecosystem to understand the underlying mechanisms causing whole system functioning (Lawton 1995). Various kinds of model ecosystems with different levels of complexity are used by ecologists, ranging from highly controlled abstract laboratory experiments to uncontrolled, highly complex, natural ecosystems. Based on the inevitable trade-off between complexity and control, ecologists have to choose appropriate model ecosystems (with an adequate level of complexity) to sufficiently answer questions of interest and at the same time to avoid over-simplification.

To study the complex adaptive character of ecosystems, natural, thus uncontrolled, ecosystems have to be preferred over highly controlled experimental systems. However, natural ecosystems are most of the time characterised by high levels of noise (unexplainable variation), which diminishes generalisations about the underlying processes causing the observable patterns (Soberón and Nakamura 2009). Nevertheless, for several natural ecosystems, like for spring fens, environmental flows of energy and matter are traceable and environmental noise is considerably dampened. Such experiment-like ecosystems provide ideal models to test ecological theories about complex systems.

Here I focus on empirical studies conducted on spring fens in the lower mountain ranges of East-Central Germany (Fig. 1). These so called 'helocrenic springs' are semi-aquatic ecosystems characterised by a spatially diffuse emergence of slow-flowing ground water which causes a contin-

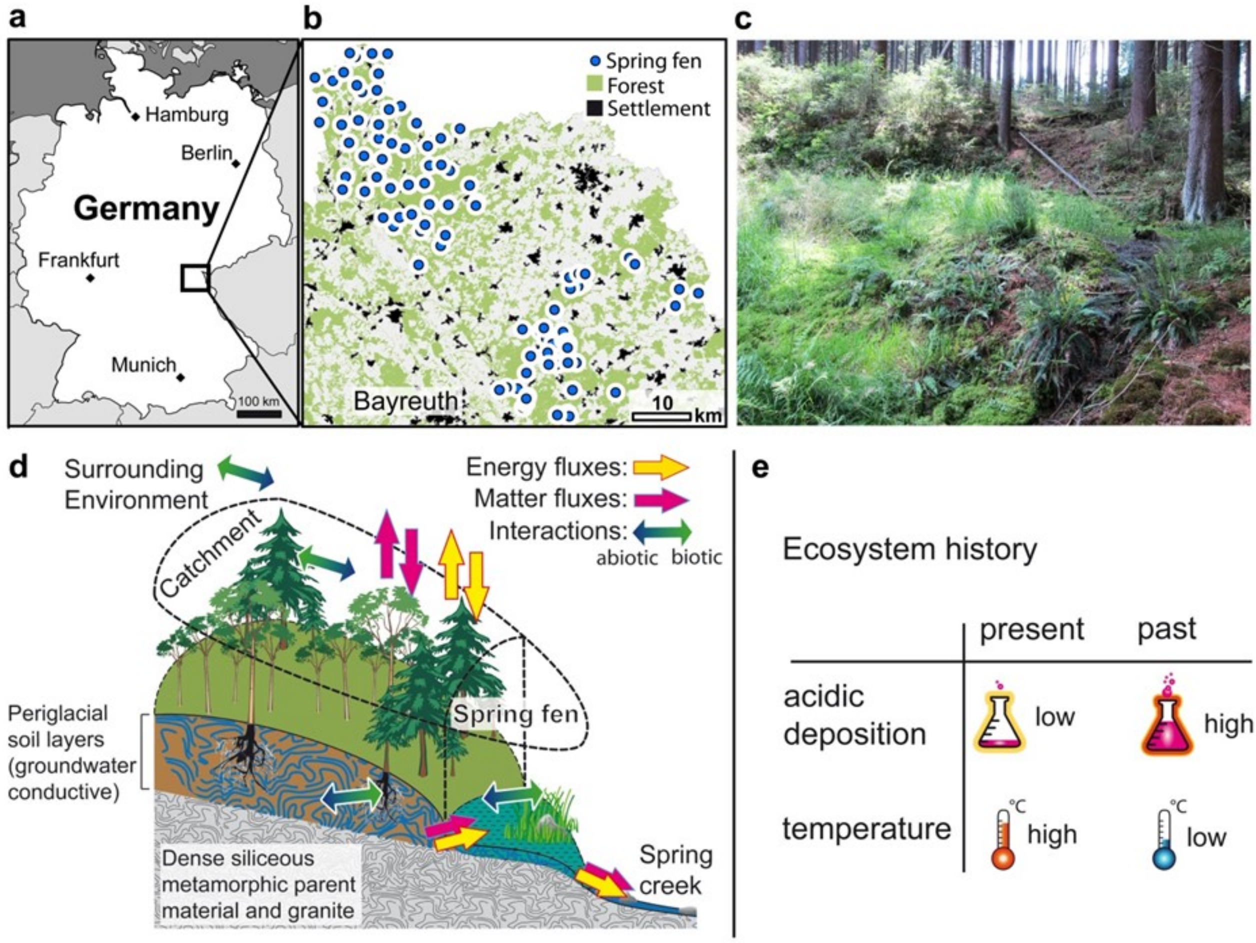

Figure 1. Spring fens as model systems to study the Complex Adaptive System theory for ecosystems. **(a)** and **(b)** The examined sites are located in the lower mountain ranges of East-Central Germany: Frankenwald and Fichtelgebirge, North-East Bavaria. **(c)** Typical spring fen appearing as a semi-aquatic island clearly demarcated from the surrounding forest vegetation. **(d)** Schematic diagram illustrating the spring fens from a systemic perspective, modified from Schweiger (2016). Although the catchment area of the spring fens provides a natural boundary, flows of energy (e.g., temperature) and matter (e.g., nutrients and acidic depositions) occur across this boundary. Abiotic changes modify abiotic and biotic interactions and, thus, change the ecological structure and processes of the subsequent spring fens. **(e)** Ecological history of the examined spring fens. Whereas acid deposition strongly decreased during the last three decades, energy fluxes related to climate change (increasing temperatures, increasing frequency of climatic extreme events) strongly increased.

uously water-saturated, marshy ground and, thus, are strongly distinguished from the surrounding, terrestrial forest habitats (Fig. 1c, Schweiger and Beierkuhnlein 2014). These ecosystems, which embody semi-aquatic islands in the terrestrial landscape, are biochemically and thermally strongly connected to a clearly delimited forested catchment (see Fig. 1d). Furthermore, the thermal and chemical conditions affecting plant species community composition in the spring fens experience relatively low temporal and spatial variation (Beierkuhnlein and Gollan 1999). The high environmental coherence and low environmental variability distinguish these ecosystems as optimal model ecosystems to empirically study interaction, adaptation and scale dependence of plant community dynamics as integrative parts of complex adaptive systems and major principles of the CAS theory (Schweiger 2016).

The high environmental coherence and low environmental variability characterising the studied spring fens are related to the physical and thermodynamic characteristics (high specific heat capacity) of water. By taking up solutes and adjusting to the temperature regime of the catchment soils, groundwater deriving from a particular catchment and subsequently feeding a particular spring fen can be seen as medium carrying information about the flow and status of energy and matter from a whole landscape unit. Beyond these facts, the examined spring fens have a significant, well documented history of environmental load (Beierkuhnlein and Gollan 1999). Acidifying atmospheric deposition culminating in Central Europe during the 1970s and 1980s, caused large-scale acidification of forest soils and massive diebacks of forests in the studied region (Matzner and Murach 1995). Significant changes occurred in the biogeochemistry of the forested catchments and groundwater chemistry feeding subsequent spring fens (Beierkuhnlein and Gollan 1999). Sulfuric depositions were significantly reduced during the subsequent years due to legal regulations, and forest and adjacent freshwater ecosystems started to recover slowly (Hruška et al. 2002). However, information about the long-term trajectories of the impacted ecosystems are largely lacking so far. Using long-term investigations about the abiotic (water physicochemistry) and biotic system characteristics and components (plant community composition) of these model systems on landscape-scales helped to fill part of this apparent lack of knowledge. Despite the relatively small size of the studied spring fens, the results obtained for these ecosystems can furthermore help to improve our general understanding about ecosystem dynamics due to the model-like characteristics of the studied spring fens.

Interaction, adaptation and scale dependence in spring fen plant community dynamics

Historic acidification is reported by several studies on these model ecosystems to affect ecosystems' response to following, external perturbations over decades, thus, highlighting the adaptive character of plant community responses to the ecosystems' environmental history (Schweiger and Beierkuhnlein 2014, Schweiger et al 2015a,b). Strong effects of previous acidification history were detected on the community organisation with three hyper-dominant (oligarchic) species with high local abundance and spatial frequency of occurrence (*Chrysosplenium oppositifolium*, *Sphagnum fallax* and *Calamagrostis villosa*; Schweiger and Beierkuhnlein 2014). All three oligarchic species characterise distinct plant community groups (different alternative states) of spring fens that were previously affected by acidification to different degrees and that reacted differently to the climatic extreme summer of 2003 as a subsequent environmental stressor. Schweiger et al. (2015a) show that spring fens previously less stressed by acidification feature higher stability to the prolonged drought and heatwave of the summer of 2003 than strongly acidified springs. These observations highlight the strong empirical link between the theoretical concepts of path dependence, stability and resilience (sensu Holling 1973) as well as alternative states in plant community composition (Beisner et al. 2003). Furthermore, we were able to show that the alternative states in plant community composition as a result of acidification history can be further stabilised by positive feedbacks between the prevalent environmental settings and ecosystem engineers sensu Jones et al. (1994), namely *Sphagnum* species (Schweiger and Beierkuhnlein 2017). These moss species, which were favoured by anthropogenic acidification, are well-known to actively acidify their surrounding and, thus, significantly affect the environmental setting for other, co-occurring species with strong effects on community structure (van Breemen 1995). Eutrophication or decreasing water tables can also increase the occurrence of *Sphagnum* species in fens (Hájek et al. 2015). Positive feedbacks between acidic conditions and biogenic habitat modification by *Sphagnum* species on the composition of co-occurring species were also reported by Peterka et al. (2014). These positive feedbacks seem to maintain alternative states in plant species composition of the examined spring fens over decades with significant effects on the community responses to subsequent climatic extreme events (Schweiger et al. 2015a).

Responses of individual plant species to environmental conditions (expressed by species occurrence in relation to temperature) furthermore turned out to be very consistent over a large span of spatial scales, from local (decimetre) to continental (i.e., Central Europe; Schweiger and Beierkuhnlein 2016). This is remarkable as the individual importance of environmental factors in driving ecological patterns like species occurrence is generally assumed to strongly vary with spatial scale (Wiens 1989, Levin 1998).

Ecological patterns (e.g., species richness) observable on small spatial scale are generally assumed to be mainly driven by biotic processes related to species-specific traits such as dispersal and competitive abilities (Pearson and Dawson 2003). When increasing spatial scale, the effect of biotic processes on ecological patterns is assumed to be increasingly averaged out and abiotic factors acting on large spatial scales (mostly macroclimate) often increase in explanatory power (Eltonian noise hypothesis, Soberón and Nakamura 2009). However, large-scale abiotic factors like macroclimate driving macroecological patterns are physically linked to micro-environmental conditions affecting ecological patterns at the community-level (Wiens 1989). Based on the observations we made for the examined spring fens, I argue that the strength of these cross-scale links between macro- and micro-environmental conditions determines whether strong scale dependence or high cross-scale similarity is observable for ecological patterns (Schweiger and Beierkuhnlein 2016). The temperature of the upwelling groundwater, which significantly affects the microclimatic conditions of the studied spring fens on the local scale (Beierkuhnlein and Graesle 1999) strongly reflects the mean annual air temperature in the catchment area (Gerecke 2016) and, thus, is linked to the climatic conditions acting on landscape to continental scale. This strong cross-scale link between micro-climatic conditions (soil temperature) on a local scale and large scale climatic conditions was also observed by Fernández-Pascual et al. (2015) for calcareous fens in the Cantabrian Mountains (Spain) and the Western Carpathians (Slovakia) although absolute temperatures differed significantly between micro- and macro-scale. However, further tests have to be conducted for other ecosystems characterised by different degrees of environmental cross-scale links to test this hypothesis about the effect of abiotic cross-scale links on the scale dependence of ecological patterns.

Outlook

The three major principles of CAS theory discussed in this article (complex interaction, adaptation and scale dependence) are subject to major interest and intensive research efforts in ecology and biogeography (e.g., Levin 1992, Pearson and Dawson 2003, Folke 2006, Siefert et al. 2012). However interactions between these principles in affecting ecosystem dynamics have rarely been tackled.

By putting together various empirical studies on plant community dynamics in spring fens I report in this synthesis the strong interaction between all three proposed principles in shaping the structure and dynamic of these model ecosystems over decades. The tight interconnection of all three principles as major parts of the CAS theory clearly shows the practical applicability of this rather abstract theoretical framework to understand ecosystem dynamics in a constantly changing, human-dominated world. However, the examined spring fens are quite exceptional in terms of their environmental characteristics which might reduce the generality of these findings. Although the investigated spring fens are reported to show high degrees of complex interactions and adaptation, low levels of scale dependence were detected, although terrestrial ecosystems are generally described to show high scale dependence of ecological patterns. Thus, the intensity to which ecosystems are characterised by interaction, adaptation and scale dependence might therefore strongly differ between different ecosystems, depending on the environmental characteristics of the particular system. In other words, the degree to which ecosystems can be described as complex adaptive systems might strongly vary for different ecosystems.

One determinant of the degree of complexity characterising a certain ecosystem could be the degree of system openness. An open system is here defined as a system where the flow of energy and matter is unrestricted between the particular system and its surroundings. Strong exchange between the system under focus and the surrounding environment will intensify abiotic cross-scale links and increase cross-scale similarity (decrease scale dependence) of species or community responses. Such exchange also will affect the complexity of interactions (strength of feedback loops) among species as well as between species and the abiotic environment. These effects on interaction complexity can in turn affect the degree of adaptive capacity a certain ecosystem can evolve against upcoming, anthropogenic changes in environmental conditions. The openness of a system mainly depends on the structural characteristics of the ecosystem which can result from abiotic (geomorphologic) characteristics (e.g., terrain roughness). Furthermore biotic characteristics of the ecosystem (e.g., vegetation structure) affecting the flow and distribution of energy and matter determine the degree of system openness. Ecosystems should therefore not be classified in a static way to be complex adaptive systems or not, but should rather be described along a gradient of complexity, adaptation, and scale dependence by considering the CAS theory as a dynamic rather than a static theoretical concept. This might help to quantify the sensibility of ecosystems to environmental perturbations in a general theoretical framework which is urgently needed in our rapidly changing world.

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