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Editorial

“Ecosystems in transition: interactions and feedbacks with an emphasis on the initial development”

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1 State transitions of ecosystems

In this Special Issue of Biogeosciences on “Ecosystems in transition: Interactions and feedbacks with an emphasis on the initial development”, we bring together research on ecosystems undergoing state transitions, including artificially created and naturally formed sites, most of them in an initial stage of development. State transitions of an ecosystem may occur either when a formerly stable system state is disturbed or when a developing system gradually achieves new functions during succession. Thus, state transitions of ecosystems are not necessarily restricted to a deterioration of ecosystems but can also be observed during initial ecosystem evolution.

The subject of ecosystem state transitions emerged in the 1970s, when the concepts of “ecosystem stability” and “resilience” were introduced to describe the risk of sudden changes of ecosystem properties (Holling, 1973). May (1977) pointed out that continuous changes of single ecosystem properties might result in abrupt changes of the whole system. More recently, Scheffer et al. (2001) developed the topic, and discussed the risk of sudden ecosystem shifts and how to manage them. Potential ecosystem state transitions have received particular attention in the context of catastrophic shifts or the breakdown of complete ecosystems. A well-known and drastic example might be the collapse of the Aral Sea during the second half of the 20th century, as documented e.g. by Singh et al. (2012). Today, against the background of global environmental change, understanding shifts in ecosystem processes and ecosystem state transitions is more important than ever.

Ecosystems may rapidly change state when certain thresholds, tipping-points or break-points are exceeded (May, 1977; Scheffer, 2001). The identification and quantification of such thresholds can be challenging, as demonstrated by Bestelmeyer et al. (2013), who found surprisingly resilient desert ecosystems during desertification experiments. López et al. (2013) investigated steppe ecosystems in Patagonia and were able to establish indices allowing them to identify critical thresholds in the transition between different ecosystem states. But there remains some controversy if such state transitions may occur abruptly after a tipping point has been exceeded. While Scheffer et al. (2001, 2009) emphasise the risk of sudden shifts in ecosystem states, Hughes et al. (2013) argue that many regime shifts happen slowly over long periods of time after a tipping point is exceeded. Such slow changes can easily remain undetected for a long time, causing delay in interventions to reverse or mitigate undesired effects.

Scheffer et al. (2001) introduced the idea that ecosystems can assume different stable states under the same climatic conditions, and that irrevocable shifts between these states can occur. There is now evidence that locations where vegetation zones can exist in such alternative stable states can be suddenly altered and shifted by climatic change (Higgins and Scheiter, 2012). Scheffer et al. (2012) investigated this type of global warming impact in boreal ecosystems. They identified two competing stable ecosystem states, tree-less tundra and different types of boreal forests, and describe the risk of substantial shifts between these biomes. Another example is the increasing global risk of desertification, which primarily results from direct human influences such as overgrazing, but is substantially aggravated by global climate change (D'Odorico et al., 2013). Rietkerk et al. (2011) discuss the importance of feedbacks between vegetation and climate processes at different scales, where local state transitions may result in system changes at larger scales. They suggest that coupling between feedbacks at different scales has to be considered and that multi-scale models are needed to appropriately predict ecosystem responses to climate change and vice versa (Rietkerk et al., 2011).

In most of the above cases, transitions of ecosystem properties are directly linked to losses of previous ecosystem functions and services and hence to degradation of the existing systems. In contrast to a negative regression combined with the loss of ecosystem functions and services, young emerging ecosystems gain new functions during succession. For example, Brankatschk et al. (2013) describe the increase of activities of different N-cycle elements during the development of biological soil crusts as early successional stages of terrestrial ecosystems: Whereas heterotrophic processes and an absence of N accumulation characterize the first stage, the mature stage of these soil crusts is similar to developed ecosystems and dominated by internal N-cycling processes. Another example is secondary succession of abandoned agricultural sites where net ecosystem production is shifting from negative (carbon losses) to positive (carbon sequestration) as demonstrated by Wang and Epstein (2013).

In many cases ecosystem state transitions are very difficult to predict, and both scientists and natural resources managers may be unprepared for early responses to change. Drivers of shifts are usually identified only in retrospect, and often with little data collected during the transition. This situation is well illustrated by long-term monitoring data from the Hubbard Brook Experimental Forest revealing the hydrological effects climate change can have on forest catchments (Groffmann et al., 2012). However, the authors emphasize that great care is necessary to interpret these ecosystem state transitions in response to natural and human disturbances. Looking for early warning signals, Scheffer et al. (2009) postulated that increasing autocorrelation in long-term time series could be such a signal. They found evidence for this hypothesis by analyzing abrupt climatic shifts in Earth's history suggesting that such shifts were often preceded by a characteristic slowing of fluctuations in measurable parameters, expressed as increasing autocorrelation (Dakos et al., 2008). On a much smaller scale, similar results were obtained by Zaplata et al. (2013), who found that transition phases in ecosystem development could be identified by increasing spatial autocorrelation among vegetation patterns. The latter study was carried out in the framework of the "Chicken Creek Project" and this Special Issue presents key findings of this project.

2 The Chicken Creek Project

Launched in 2005, the objective of the Chicken Creek Project is the study of ecosystem transitions during the initial phase of development. The investigations are based on the artificial watershed Chicken Creek (State of Brandenburg, Germany) for a catchment-scale case study of ecosystem development starting from a well-defined initial state with no vegetation on undeveloped soil and with a bottom liner as a well-defined hydrological lower boundary condition (Elmer, 2013; Gerwin et al. 2010). Additional studies were performed on young ecosystems created by natural processes such as the Damma Glacier forefield in Switzerland (Bernasconi et al., 2011; Dümig et al., 2011, 2012). A first phase of the project was finished in 2012.

The overall objective of the first phase of the Chicken Creek Project was the identification of developmental stages and feedbacks associated with the emergence of new system states that could be applied also to ecosystems in general. It was hypothesized that the initial phase in the development of an ecosystem is characterized by less structure, heterogeneity and complexity than later phases and that the analysis of young ecosystems in their initial stages thus could provide better insights into ecosystem functioning (Schaaf et al., 2011; Raab et al., 2012). Further, the characteristics of ecosystem structures and processes can be interpreted as indicators of the state of the whole system. The following three system categories may be distinguished in the sequence of stages during early ecosystem development: (1) a more or less abiotic geo-system, followed by (2) a hydro-geo-system and eventually (3) a bio-hydro-geo-system (Schaaf et al., 2011).

The Chicken Creek ecosystem development was unexpectedly rapid in the very first years, showing a surprisingly fast increase in complexity of patterns and structures in this process (Gerwin et al., 2011; Elmer et al., 2013). The project demonstrates that artificial landscape units like the Chicken Creek catchment are perfectly appropriate to be used as observatories for studying initial stages of ecosystem development in their full complexity under real-world conditions. In addition, artificial ecosystems are particularly well suited to communicate ecosystem research to the general public.

3 Initialization of ecosystems and the initial development phase

The initial state of an ecosystem, as represented by the Chicken Creek catchment, can result from severe disturbance destroying a previous ecosystem. In contrast to frequent "normal" disturbance regimes, large, infrequent disturbances (LIDs) are defined as events that result in complete degradation of an ecosystem (Turner and Dale, 1998) and put an ecosystem back to "point zero". Well-known studies dealing with the effects of LIDs on ecosystems are the investigations at Surtsey Island near Iceland in the 1960s and 70s (Friðriksson, 2005) or the research conducted on ecosystem recovery following the eruption of Mount St. Helens (USA) in the 1980s (e.g. Bishop, 2002; del Moral and Bliss, 1993). This research brought important insights into primary succession processes, particularly from a biological point of view. In general, only limited interdisciplinary knowledge exists on the very initial phase of ecosystem development, although the course of development at this stage may play a decisive role for the development at later stages. Even "small differences early in the process can ramify over time", as pointed out by Walker and del Moral (2003, p. 329).

The central question here is: What is specific for the initial phase of ecosystem development, and how can its end be defined? Walker and del Moral (2003) stated that the end of primary succession and the beginning of secondary succession lack proper definitions. With regard to the development of vegetation cover, they conclude that primary succession can be considered complete "if vegetation change (or any other parameter of interest) is slowed and a relative equilibrium exists for an extended period of time" (Walker and del Moral, 2003, p. 12). In a similar way, Raab et al. (2012) tried to define the initial phase of the development of an ecosystem as the highly dynamic period of time between a severe disturbance event and the establishment of a first dynamic equilibrium with regard to element cycling. However, primary succession is not always linear and a well-defined equilibrium as the endpoint of initial ecosystem development will only rarely exist (Walker and del Moral, 2003).

White and Pickett (1985) characterized disturbances that cause the initialization of an ecosystem as relatively discrete events in time altering, e.g., resources or substrate availability. Based on this, we suggest an additional definition for the initial state of ecosystems: *An initial ecosystem is characterized by a recent discontinuity in its abiotic site conditions compared to a previous state. This discontinuity is resulting from a severe disturbance that altered the parental material by removing and relocating the existing soil, or by accumulating allochthonous substrates*. Therefore, the new ecosystem is not directly linked by "geological memory effects" to structural properties of the previous ecosystem, in contrast to systems undergoing a secondary succession that are shaped by structures remaining from the preceding system. As a consequence, initial ecosystems are typically disconnected from their surroundings and exhibit "island" properties.

In this regard, it can be relevant whether the discontinuity in the development of the substrate is due to natural or anthropogenic factors. In case of a natural disturbance, the new ecosystem is more likely to develop similar properties with time as surrounding mature ecosystems, because if there are undisturbed sites in the neighborhood with similar geological conditions plants and animals can invade from there. Such allochthonous control of primary succession can be found e.g. in cases of ecosystem destruction due to volcanic activities as described by Mueller-Dombois and Boehmer (2013) in this issue. In contrast, human disturbances are often associated with the deposition of substrates that are very different from those of the surroundings as for example in mining landscapes. In that case, ecosystem development will be more isolated from neighboring ecosystems, and thus is likely to be more autochthonous and exhibiting stronger island effects. Generally, it can be expected that primary succession is less predictable the larger the disturbance was that destroyed the previous ecosystem and the more dissimilar the substrate of the newly developing ecosystem is from the surrounding ecosystems (Turner et al., 1998).

Following Hartvigsen et al. (1998), ecosystems can be considered classic examples of complex adaptive systems (CAS), which are systems with a large number of interacting and adapting components, also called "agents". There are many other types of CAS apart from ecosystems (Holland, 2006). With regard to ecosystems, Levin (1998) pointed out that aggregation and assembly of agents during ecosystem genesis could be understood as the result of self-organization processes. While these processes also govern the later development of the system, the local rules of interactions among agents will change during the system's evolution resulting in potentially alternative stable states. Being self-organizing adaptive systems, ecosystems gain resilience against disturbances, in contrast to intensively managed systems in agriculture or forestry (Levin, 1998). Marsh ecosystems provide an illustrative example for increasing resilience during initial ecosystem development resulting from self-organization. According to a recent study by Marani et al. (2013), marsh vegetation inadvertently "engineers" the landscape by a system of feedbacks that results in tuning soil elevation within preferential ranges of optimal adaptation. Rietkerk et al. (2011) give further examples in which vegetation functions like an "ecosystem engineer" by means of feedback loops adapting the abiotic environment in a way that improves the conditions for its own survival.

4 This Special Issue – case studies of initial ecosystems

This special issue presents a collection of observational and experimental studies that focus on processes occurring during state transitions in the development of ecosystems and provide insights into the feedback mechanisms controlling them. These state transitions are studied at multiple scales, ranging from the pore scale to the catchment scale. The contributions collected in this issue can be divided into two main groups: (i) studies dealing with state transition occurring in initial ecosystems without active human interference, and (ii) studies dealing with active restoration of ecosystems after severe disturbances.

In the first group of papers, several contributions deal with microbial processes during initial ecosystem development. Schulz et al. (2013a) provide a general review on the role of microorganisms for initial soil development emphasizing the importance of well-established biotic-abiotic interactions for ecosystem functioning. Two other papers by Schulz et al. (2013b) and Esperschütz et al. (2013) present findings with regard to N-fixation and litter decomposition in early state ecosystems. Risse-Buhl et al. (2013) show the importance of "old" inherited organic carbon for young ecosystems as a nutrient source for microorganisms. Another group of papers addresses feedbacks between abiotic and biotic structures and the formation of patterns during ecosystem development. Fischer et al. (2012) show that biocrusts developing on bare surfaces of initial soils can have direct feedbacks effects on physical site conditions. Biber et al. (2013) analyze relationships between initial site conditions and evolving vegetation patterns, whilst Felderer et al. (2013) investigate strategies of plants to forage for phosphorus as a soil nutrient that is often of very low availability in initial ecosystems. Finally, Mueller-Dombois and Boehmer (2013) summarize the long-term primary succession of Hawaiian rainforest ecosystems which may serve as reference sites for initial ecosystems due to frequent disturbances by volcanism.

The other papers deal with examples of management practices for ecosystems after severe disturbance. Papers by Audet et al. (2013); Cohen-Fernández and Naeth (2013) and Quideau et al. (2013) highlight various aspects, methods and boundary conditions of mine site restoration in Australia and Canada. The overall aim of mine site restoration is the rapid establishment of desired target vegetation or the acceleration of natural revegetation. The success of such restoration depends on many factors, and the paper by Schulz et al. (2013a) comes to the conclusion that "simple" management strategies like reforestation, irrigation or fertilization do not guarantee accelerated ecosystem development, as biotic-abiotic interactions still have to establish at very young sites, which requires better understanding of the specific functioning of initial ecosystems.

5 Central findings from initial ecosystem research

The examples presented in his Special Issue support the above suggested importance of geological discontinuities and substrate properties for initial ecosystems as introduced in the definition. Particularly the example of the Hawaiian rainforest evolution and its reaction on disturbances by volcanic activities illustrates the initialization of ecosystems by geological processes (Mueller-Dombois and Boehmer, 2013, this issue). Highly complex process networks and abiotic-biotic interactions are active during initial ecosystem development to transform substrates to soils as described by Schulz et al. (2013a) in this issue. This central importance of substrate quality for ecosystem development is also reflected by the enormous efforts necessary to enhance and accelerate soil development during restoration as shown by Quideau et al. (2013) and Cohen-Fernández and Naeth (2013) also in this issue.

However, understanding the dynamics of initial ecosystem development still remains a challenge. Many interactions between structures and processes as well as feedbacks of the initial ecosystem phase are still unclear. The mentioned Chicken Creek project led to a number of results that are of importance for the understanding of initial ecosystem state transitions (see Hüttl et al., 2013): It was found that the basic assumption of low heterogeneity and structuring of ecosystems in their initial stage was essentially correct. Though small, it seems that these heterogeneities were of great importance for the later development of the system, however, as highlighted by Felderer et al. (2013) and Biber et al. (2013) in this issue. This relates to earlier publications from the Chicken Creek project, which show that slight differences in substrate properties influenced hydrological pathways, such as erosion rill patterns (Hofer et al., 2012) and groundwater flow patterns (Hofer et al., 2011).

In addition, papers of this issue show that soil crusts of both physical and biological nature can be of great importance in initial ecosystems also in a temperate climate (Schulz et al., 2013a, Fischer et al., 2012). Such crusts tend to promote surface runoff due to soil surface sealing, which impedes water infiltration as shown earlier by Fischer et al. (2010). Given a lack of preferential flow paths created by burrowing soil fauna (Badorreck et al., 2012) or root channels, they could explain why surface runoff can be unexpectedly high and potentially underestimated in modeling attempts of initial systems (Holländer et al., 2009).

Another important finding from the Chicken Creek catchment reported in this issue is the role of "old" organic carbon in initial ecosystems (Risse-Buhl et al., 2013), a phenomenon that had also been observed in other types of young ecosystems (Hood et al., 2009; Guelland et al., 2013). This importance of allochthonous material for initial microbial processes corresponds to the findings Schulz et al. (2013a) presented in this issue. They show that the initial nitrogen budget was found to be dominated by decomposition of deposited organic compounds in the Damma glacier forefield (see also Brankatschk et al., 2011).

It can be summarized that proper prediction of development and responses of landscapes, particularly under global change conditions are still limited. However, for improved ecological restoration and management approaches knowledge of structures and processes during the initial development of the ecosystem is necessary. Studies of initial ecosystems like those presented in this Special Issue may help to deduce required new theoretic ecological concepts.

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