Resilience, Integrity and Ecosystem Dynamics: Bridging Ecosystem Theory and Management

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Abstract In this paper different approaches to elucidate ecosystem dynamics are described, illustrated and interrelated. Ecosystem development is distinguished into two separate sequences, a complexifying phase which is characterized by orientor optimization and a destruction based phase which follows disturbances. The two developmental pathways are integrated in a modified illustration of the "adaptive cycle". Based on these fundamentals, the recent definitions of resilience, adaptability and vulnerability are discussed and a modified comprehension is proposed. Thereafter, two case studies about wetland dynamics are presented to demonstrate both, the consequences of disturbance and the potential of ecosystem recovery. In both examples ecosystem integrity is used as a key indicator variable. Based on the presented results the relativity and the normative loading of resilience quantification is worked out. The paper ends with the suggestion that the features of adaptability could be used as an integrative guideline for the analysis of ecosystem dynamics and as a well-suited concept for ecosystem management.

Keywords Orientor · Resilience · Adaptability · Ecosystem integrity · Ecosystem indicators · Disturbance

1 Ecosystems are Dynamic Systems, and So are their Scientific Perceptions

Although the term "ecosystem" has an age of only 70 years since Tansley's grounding in 1935, the fundamental understanding of ecosystem dynamics has been based upon a multitude of consecutive ideas. If we take a look back to the second half of the last century, the idea that increased complexity automatically leads to increased *stability* was a "conventional wisdom" in ecology (Begon et al. 1990). Elton's

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respective arguments from 1958 supported the development of the long-term dominating stability paradigm: Ecosystems have to be managed in a way that guarantees their *stability*, *resistance* and *robustness*.[1] These ideas were promoted accessory by the application of cybernetic approaches in ecology. They are founded on the concept of *equilibrium*, and thus the inherent target of an object was comprehended as its ability to return to the initial state after any perturbation (Grimm and Wissel 1997; Joergensen and Straskraba 2000).

In the 1970's these convictions became *vulnerable* and *fragile*. Initially, succession analyses and theories demonstrated that there are constructive pathways of (instable) dynamics in ecosystem history (Odum 1969), valuing mature states as the final developmental targets. Nearly simultaneously, the model experiments of May (1972) had shown declines of local stability with complexity. Besides the correlated doubts in the stabilizing functions of biodiversity, thereafter the whole stability concept became open to attack. Thermodynamic investigations demonstrated that in nature *irreversible* (and therefore instable) reactions are dominant (Prigogine 1980), and chaos and catastrophe theory emphasized the unpredictability of ecosystem states, thereby undermining important stability statements and opinions (Joergensen and Müller 2000). *Disequilibrium* theories were developed (Schneider and Kay 1994), and the new *resilience* paradigm started its development after Holling's paper (1986) about local surprise and global change. Destruction became an accepted agent of evolutionary development, and the perception of change has been altered totally, temporary ending in the panarchy theory of Gundersson and Holling (2002). Typically enough, this theory has been nominated with reference to the Greek god Pan, who feels responsible for the power of nature as well as panics and destabilisation. Thus, finally, we have returned to the knowledge of the Greek philosopher Heraclitus who stated that *nothing is permanent but change* already 500 years BP. Today this recognition is being claimed by the United Nations, postulating that "ecosystem change is inevitable" in their CBD ecosystem approach (see Müller and Burkhard 2007) which functions as a guideline for nature protection.

Remembering these historical trails in science, the appreciation of ecosystem dynamics provides a metaphoric example for the dynamics of the natural systems themselves: We will find no stability at all, "everything is flowing", and the question is whether the concept of resilience is able to provide better answers.[2] Referring to the recent situation we want to illuminate some components of the described "adaptive knowledge cycle" and discuss the following questions:

- Is there a general tendency in undisturbed ecosystem development?
- How can this trend be indicated?
- Which is the role of disturbance throughout ecosystem dynamics?

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[1] several technical terms from systems theory and resilience research are defined briefly in Box 1.

[2] At least it is providing many answers, moving from 50 topical publications in 1992 to more than 250 in 2006 (Janssen 2007) and increasing the scientific and communicative complexity enormously. Thus the resilience concept is developing in a scientific version of orientor dynamics.

- What are the recent comprehensions within the resilience and adaptability concept?
- Is there a potential to quantify these attributes?

2 Ecosystems Follow Orientor Dynamics and Increase Complexification

Now – being aware of the uncertainty and vulnerability of scientific statements – the first of these questions can be discussed. In fact even throughout the dynamics of paradigms as they are described above, typical developmental patterns can be found. In ecosystems, different kinds of successions (autogenous vs. exogenous, primary vs. secondary, progressive vs. retrogressive successions) take place as ordered processes of community development at varying temporal and spatial scales (Walker and del Moral 2003; Walker et al. 2007). Changes in community structures cause changes in the physical ecosystem functions (e.g., energy budget, water and matter cycling), and these modifications vice versa cause changes of the system's processors composition, its content of information and the degree of complexity. In the end, usually a number of similarities appear in successions, leading to the typical sequences of pioneer, middle aged and mature ecosystems, which Odum has compiled in 1969. Due to individual exterior inputs, to the dynamics of constraints,

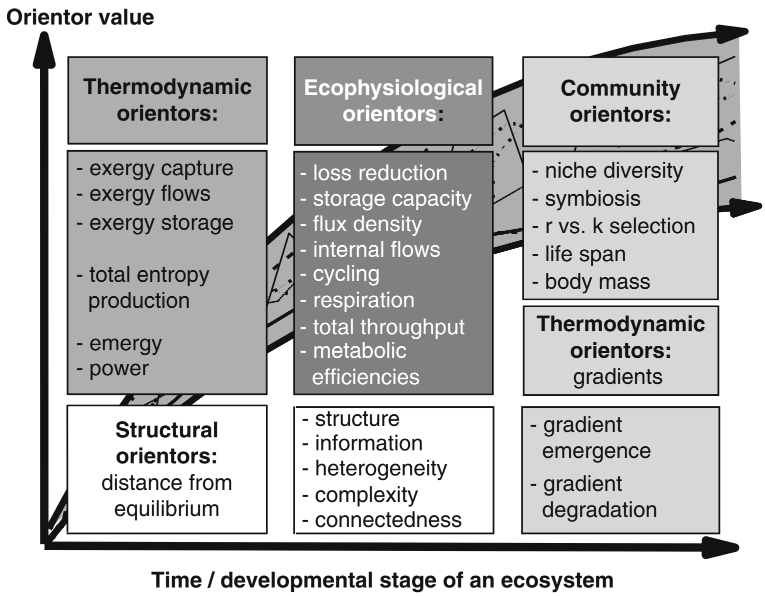

Fig. 1 Some ecosystem orientors: If an ecosystem develops in an undisturbed manner the values of the orientor variables will be optimized until they reach a site specific maximum. For further information see Joergensen et al. (2007)

Box 1: Glossary; more detailed definitions can be found in the text

Adaptability	A system has a high adaptability if the sum of all disturbances and changes in the attractor domains do not reduce the system's degree of self-organization.
Adaptive cycle	The adaptive cycle is a metaphor and a conceptual model of cyclic developmental phases of ecosystems and socio-ecological systems. The identified phases are: growth or exploitation, conservation, collapse or release, and reorganization (Holling et al. 2002).
Disturbance	Any relatively discrete event in space and time that disrupts ecosystem, community, or population structure and changes resources, substrates, or the physical environment is called disturbance (Picket and White 1985).
Ecosystem integrity	Integrity is a management target to support and preserve those processes and structures which are essential prerequisites of the ecological ability for self-organization (Barkmann et al. 2001).
Orientor	Orientors are indicating ecosystem components which are generally optimized throughout undisturbed successions.
Panarchy	Panarchy is the temporal structure in which systems are interlinked in continual adaptive cycles of growth, accumulation, restructuring, and renewal (Gundersson and Holling 2002).
Resilience	Resilience refers to the ability of a system to reorganize after a disturbance and remain in the previous basin of attraction.
Resistance	Resistance characterizes a system which is not influenced by a disturbance.
Robustness	Robustness refers to the capacity of a system to maintain the structure despite perturbations (Gallopin 2006).
Self-organization	Self-organization is the spontaneous creation of macroscopic order from microscopic disorder, whereby structural and functional gradients are created.
Stability	Stability is the ability of a system to return to an equilibrium state after a temporary disturbance (Holling 1973).
Vulnerability	Vulnerability is the exposure to contingencies and stress, and the difficulty in coping with them as a function of sensitivity and resilience (Millennium Ecosystem Assessment 2005).

and to the high degree of developmental uncertainty, maturity must be characterized as an attractor function. The concrete values of development-based indicators cannot be foreseen, and some communities even never reach the climax stage (see Fig. 1). But the general direction of that development is a clear consequence of self-organization.

In order to describe and evaluate ecosystems' developmental stages and their varying properties, *ecosystem orientors* have been proposed as indicating criteria of ecosystem states, realizing the inherent uncertainties (Müller and Leupelt 1998). Depending on the investigated dynamics and processes, different types of orientors have been defined, such as thermodynamic orientors, network orientors, ecophysiological orientors, eco-dynamic orientors and community orientors (see Fig. 1). Based on non-equilibrium thermodynamics (Joergensen 2000; Schneider and Kay 1994; Kay 2000), network development (Fath and Pattten 1998) and succession theory (e.g., Odum 1969), the *orientor approach* was developed as a systems-based outcome from the theory of self-organized ecosystem dynamics (Bossel 1998, 2000; Müller and Leupelt 1998).

The succeeding processes are based on the fact that self-organised entities like ecosystems are able to generate structures and gradients if exergy passes through the system. Exergy is the energy fraction of a system which can be converted into other forms of energy or mechanical work (Joergensen 2000). During the development, gradients and structures are built up, maintained and operated, transforming the incoming exergy (e.g., high frequency solar radiation) within metabolic reactions into non-convertible energy fractions (entropy production; e.g., CO_2 or heat from respiration). Thereby, parts of the captured exergy are stored as biomass, detritus and information. These processes of ecosystem development, including phases of exploitation, growth, and conservation, characterize a development towards an attractor state of high complexity and connectivity. Developments towards attractor states and related orientor dynamics are – in general – associated with increase of stored biomass (captured exergy, see above), more complex food webs, more diversity in species and habitats, more matter cycling and reduced nutrient loss. These developments take place in long-term trajectories on varying spatial scales (see Fig. 1 and Table 2).

What does this mean for environmental indication and management? In the following chapter we will try to build a bridge and make those theoretical conceptions applicable.

3 Ecosystem Integrity Indicates Orientor Development

To describe orientor dynamics towards maturity, comprehensive sets of long-term data from different sites at varying conditions are needed. Alternatively, or in addition, model simulations can be used for respective quantifications. As the number of elements and processes that can be measured or modelled is however limited, applicable assessments have to be based on a selected set of manageable indicators, representative for the system in focus. Nevertheless, respective indicators have to denote ecosystem processes (such as energy, matter and water budgets and cycling) and structures (abiotic and biotic components) as a whole in order to assess and evaluate the system's stage of self-organization (Müller 2004, 2005). An overview of such indicators is given in Table 1. Exemplary applications in case studies will be described later on.

The resulting indicators are representatives for orientor dynamics in ecosystems. Thus, they provide information about the developmental stage and the degree of self-organization of ecosystems and landscapes. If needed, a comparison of the actual developmental stage with an observer-defined (and thus, normative) mature or target stage can be made. By doing so, estimations of potentials for future self-organization can be suggested.

The developmental contexts and variables described above have also been used in environmental management. The respective concepts of ecosystem health (e.g., Rapport and Moll 2000) and integrity have been discussed intensively in the last years. Ecosystem health and integrity are comparable concepts, representing the

Table 1 Selected indicators of ecosystem integrity in the wetland case study

Ecosystem component	Indicator
Biotic structures	Number of plant species
Energy budgets, exergy capture	Net primary production (NPP)
Energy budgets, entropy production	Microbial soil respiration (MSR)
Energy budgets, metabolic efficiency	NPP/soil respiration
Hydrological budgets, biotic water flows	NPP/transpiration
Chemical budgets, nutrient loss	Net nitrogen mineralization (NNM)
	Nitrate leaching
	Denitrification
Chemical budgets, storage capacity	Nitrogen balance
	Carbon balance

same concern: a system based description of environmental entities to support ecosystem functioning (Rapport 1989; Haskell et al. 1993). The term "integrity" has been introduced by Leopold (1944) to characterize requirements for the stability of biotic communities. During the last decades the concept has been further developed, e.g., by Woodley et al. (1993), Westra and Lemons (1995), Crabbé et al. (2000) and Barkmann (2002). In some of these interpretations integrity is strongly related to the idea of wilderness, other authors refer to a normative, social perspective, and in a third group of interpretations integrity represents a complex systems approach, which is mainly based upon variables of energy flows, matter budgets and structural features of whole ecosystems (Barkmann et al. 2001).

Taking into account the contexts described above, it becomes clear that the ability for future self-organizing processes within the respective system has to be preserved (Kay 1993). Ecosystem integrity thus describes ecosystem functionality as a result of self-organized dynamics. Applying this viewpoint, Barkmann et al. (2001) have defined the management target of ecological integrity as "a support and preservation of those processes and structures which are essential prerequisites of the ecological ability for self-organisation".

4 Disturbance Causes Stress and Innovation

In the preceding chapter, the focus has been put on growth and development processes in ecosystems. In fact, these are important features of ecosystem dynamics. Most of its life time the system follows these traits, and they provide the origins of various emergent ecosystem properties. But the picture remains totally incomplete if disturbance and decay are not taken into account (Joergensen et al. 2007). These putatively "destructive" processes can be observed on all relevant scales: For example, death and decay of organisms and their components are integral elements of natural dynamics, populations have limited life spans at certain places, and also ecosystems themselves exist for a limited period of time only. The disturbing processes can be observed on many different scales, as results of climatic changes, shifts of biomes, or as continuous invasions of new species. On the contrary, abrupt processes often modify ecosystems very efficiently within rather short periods of time. Besides many different human interventions, also “natural” disturbances can be found, such as volcanic eruptions, droughts, soil erosion events, avalanches, landslides, fires, windstorms, pests, or pathogen outbreaks. The consequences of such rare events can be enormous (see Picket and White 1985; Scheffer and Carpenter 2003; White and Jentsch 2001; Joergensen et al. 2007).

If we apply these general points to the conceptions mentioned before and if we restrict our argumentation to natural phenomena, it can be stated that two general processes are governing the dynamics of ecosystems: On the one hand, there are long phases of *complexification*: starting with the pioneer stage, orientor dynamics bring about slow mutual adaptation processes with long durations, if there is a dominance of biological processes. A system of interacting structural gradients is created, which provoke very intensive internal flows and regulated exchanges with the environment (Müller 1998). The processes are linked hierarchically (Müller 1992), and the domain of the governing attractor remains rather constant, whereupon optimization reactions provoke a long-term increase of orientors, efficiencies and information dynamics.

The highest state of internal mutual adaptation is attained at the *maturity* domain. But the further the system has been moved away from thermodynamic equilibrium, the higher seems to be the risk for the system of getting moved back (Schneider and Kay 1994). The more time has been used for complexification, the higher is the risk of being seriously hit by disturbance, and the longer the elements of the system have increased their mutual connectedness, the stronger is the mutual interdependency and the total system’s brittleness (Holling 1986). In general it can be concluded that the ability to adapt after changes of the constraints may be decreased when a high degree of maturity is attained. The respective system features have been arranged in Table 2.

In Fig. 2, the sequence of ecosystem states has been illustrated as a function of the system’s internal connectedness and the stored exergy, in parallel to the adaptive cycle from the resilience alliance (Gundersson and Holling 2002). Starting with the exploitation function, there is a slow development. The trajectory demonstrates a steady increase in mutual interactions as well as an increase in exergy stored. As

Table 2 Compilation of basic phases in ecosystem development and some summarized ecosystem features, after Holling (1986) and Joergensen et al. (2007)

Developmental stage	Productivity	Connectivity and self-regulation	Nutrient loss	Flexibility
Start	Low	Low	High	High
Fast growth	High	Low	High	High
Fast development	Decreasing	Increasing	Decreasing	Decreasing
Maturity	Low	High	Low	Low
Breakdown	Low	Low	High	High
Reorganization	Low	Low	High	High

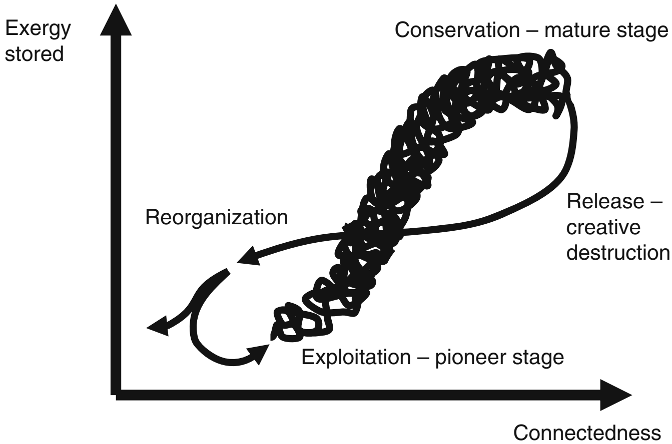

Fig. 2 Ecosystem trajectories of connectedness and stored exergy, after Holling (1986) and Joergensen et al. (2007)

has been described above, this energetic fraction can be distinguished into a material fraction and the specific exergy which refers to a complexification of the system's structure. In spite of several variabilities (e.g., annual cycles), the long term development shows a steady increase up to the mature state. Here the maximum connectivity can be found, which on the one hand is a product of the system's orientation, but which also is correlated with the risk of missing adaptability that has been nominated as overconnectedness by some authors. After the fast releasing event, the short-term conditions determine the further trajectory of the system. It might turn into a similar trajectory or find a very different pathway.

Throughout the introduction of disturbance it was mentioned that destruction and decay take place on multiple scales. Now we can extrapolate this fact to the "adaptive cycle" of Fig. 2: All ecosystem components potentially develop with the described phases, and many ecological processes support these dynamics. Observing this context from a hierarchical viewpoint, four different elements with typical frequencies and amplitudes may be distinguished:

- The dynamics of constraints
- The inherent dynamics of the focal variable
- The dynamics of the underlying fast processes
- The dynamics of the disturbance itself

The performance of the ecosystem arises from the complex interactions of these components. And furthermore, the long-term development of a system itself can be viewed from a hierarchical viewpoint: Within certain thresholds the ecosystem (as a focal level of observation) can follow the changes of the constraints. Due to the internal "brittleness" there will be a breakdown, if the constraints change or if a disturbance appears. In this situation the "creative destruction" may enable the system to start a reset under the new prevailing conditions. If the respective state variables are able to return to orientor dynamics, in the end disturbance can be understood as a part of ecosystem growth and development on a higher temporal scale; disturbance may even be extremely necessary to enable a conituation of the complexifying trajectory of the overall system. Disturbance thus can cause stress, it can support adaptation and it may create innovative structures. Of course, on the other hand many disturbances, i.e., the consequences of human interventions, can set the system back to a less complex state, with minor mutual adaptations and a reduced diversity, thereby reducing the options of future emergence of complexity. Therefore, it might be helpful to take a look at the prevailing definitions of the respective variables of ecosystem dynamics and to introduce the concepts of resilience and adaptability, which have been elaborated on the base of the "adaptive cycle" concept.

5 Elements of Ecosystem Change Can be Characterized

The recognition that permanent stability is an unattainable state for ecosystems has caused a long lasting debate about how the diverse changes that occur following a disturbance can be characterized. This chapter gives an overview about the numerous concepts that have been developed in order to characterize changes and responses to disturbances, focusing on the concepts of resilience, adaptability and vulnerability.

An ecosystem can respond to a disturbance in two opposite ways. Either it stays essentially the same without structural changes, or it collapses into a qualitatively different state. The first reaction is commonly assigned to a resilient system with adaptive capacity, the second one to a vulnerable system. But there is a variety of definitions that concretize these concepts, without an overall consensus on their meanings (Brand and Jax 2007). However, there seems to be an agreement that "vulnerability is not always a negative property" (Gallopin 2006) and "resilience is not always a good thing" (Walker et al. 2004).

The term resilience has been used in various disciplines (see Table 3). It was introduced to ecology by Holling (1973) who illustrated in his paper "resilience and

Table 3 Utilization of the term "resilience" in different scientific and applied disciplines

Physics	Material resilience: capacity of a material to absorb energy when it is deformed elastically (Joergensen et al. 2007)
Network theory	Network resilience: ability to provide an acceptable level of service in the face of various faults (Najjar and Gaudiot 1990)
Industry	Engineering resilience : create processes that are robust and flexible (Hollnagel et al. 2006)
Psychology	Resilience: capacity of people to cope with stress and catastrophe (Luthar et al. 2000)
Economics	Resilience: ability of a local economy to retain function, employment and prosperity in the face of perturbations (Farber 1995; Briguglio 2004)

stability of ecological systems" the existence of multi-stable states of ecosystems and thereby prepared an end of the perception of single equilibria and global stability. He states that "resilience determines the resistance of relationships within a system and is a measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist" whereas stability is "the ability of a system to return to an equilibrium state after a temporary disturbance". In his definition, resilience refers to a dynamic system far from equilibrium whilst stability refers to a system close to an equilibrium state (Gunderson, 2000). There are, however, other definitions of resilience that are similar to the stability concept and assume only one stable steady state, e.g., the definition of Pimm (1984) which calculates resilience as the return times of variables "towards their equilibrium following a perturbation". This conception has later been termed "engineering resilience" by Holling (1996).

More recent definitions of resilience presume the existence of multiple stability domains, but extend Holling's (1973) definition by including hierarchy, cross-scale interactions and the theory of complex adaptive systems, thereby intermingling the concepts of resilience and adaptability (e.g., in Gunderson and Holling 2002; Walker et al. 2004). These definitions are called "ecological resilience" in contrast to the "engineering resilience". An often cited definition of ecological resilience is that of Walker et al. (2004) who characterize resilience as "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks". Hence, the focus in this definition is on the maintenance of functions and structure of an ecosystem. Walker et al. (2004) specify four aspects of resilience which they also use to characterize the "basin of attraction", that is the sum of all attractors that induce the system to tend toward an equilibrium state. Accordingly, the first aspect of resilience is latitude, or the maximum amount a system can be changed before losing its ability to recover. Assigned to the basin of attraction, this aspect refers to the width of the basin. Resistance, the second aspect, is defined as the difficulty of changing the system, or the depth of the basin of attraction. The third aspect, precariousness, is the proximity of the system to a threshold, and the last one, panarchy, refers to influences of systems of another hierarchical level.

The resilience-perception of Carpenter et al. (2001) builds a bridge to the concept of adaptability. They define resilience as being composed of the following three properties:

(1) the amount of change the system can undergo and still remain within the same domain of attraction,
(2) the degree to which the system is capable of self-organization, and
(3) the degree to which the system can build the capacity to learn and adapt.

The adaptive capacity that Gallopin (2006) equates with the term adaptability, therefore is a component of resilience sensu Carpenter et al. (2001), but the relation between adaptive capacity and resilience, the question of which one is an element of which, remains unclear "because of the diversity of views" (Gallopin 2006). For instance, the perception of Norberg and Cumming (2006) that adaptive processes relate to the capacity to tolerate and deal with change and those of Smit and Wandel (2006) that adaptive capacity allows for continuous development, resemble the above mentioned definitions of resilience. Thus, it doesn't become clear if resilience includes adaptability or is a component of the latter.

Both concepts are by now used in various disciplines and frequently applied to social-ecological systems (e.g., in the journal Ecology and Society 11, 2006). Here, the distinction between resilience and adaptability is clearer, due to the definition of Walker et al. (2006) that determines adaptability to be the capacity of the actors in a system to influence resilience. Social-ecological systems are, however, not the subject of this article and in spite of the inherent commendable distinctions, the applicability as well as the precision of this definition may be observed with some doubts.

Now, how does the previously mentioned term "vulnerability" of an ecosystem fit into this mess of definitions? Just as the relationship between resilience and adaptability, the linkage of both concepts with vulnerability remains unclear. Smit and Wandel (2006) identify three elements of vulnerability, which are

(1) sensitivity,
(2) adaptive capacity, and
(3) exposure.

Hence, adaptability is seen as an element of vulnerability. Sensitivity, the first element of vulnerability, has been defined by Gallopin (2003) as the "amount of transformation of the system per unit of change in the disturbance" and exposure – the last element – is defined by Adger (2006) as an "attribute of the relationship between the system and the perturbation", therefore the exposure is not an internal property of the system, but a characteristic of the relationship between the system and the disturbance (Gallopin 2003). This is the reason why Gallopin (2003), unlike Smit and Wandel (2006) does not consider the exposure to be an element of vulnerability. Also the relationship between resilience and vulnerability is being discussed by several authors (Gallopin 2003, 2006; Walker et al. 2004; Young et al. 2006; Smit and Wandel 2006). There is an agreement, that both attributes are ambivalent (Walker et al. 2004) insofar as a resilient system is less vulnerable than a non-resilient one (Gallopin 2006). In other words, a system that reacts vulnerably to a disturbance changes its structure and functions, whereas a resilient system does not. The question emerges from this statement, if vulnerability is the opposite of resilience. Gallopin (2006) concludes that the ambivalent relationship between both does not imply symmetry, since resilience applies to the system's persistence in the considered domain of attraction while vulnerability refers to transformations that change the system fundamentally and may go beyond a single domain of attraction. According to Gallopin (2006) the opposite of vulnerability would rather be robustness, which refers to the capacity to maintain the structure despite perturbations.

It becomes obvious that the terms of resilience, adaptability and vulnerability are not clearly distinguished in existing definitions but are often used interchangeably (Gallopin 2006). They are used in a very wide extension and are affected by a conceptual vagueness (Brand and Jax 2007) that hinders their practical application. Brand and Jax (2007) also criticize the increasing degree of normativity in current definition and group the existing definitions in descriptive, hybrid (descriptive-normative), and normative definitions.

Another problem of application is the missing definition of the terms identity, structure and functions, and basin of attraction, which should all be maintained in resilient systems. Carpenter et al. (2001) therefore ask "resilience of what to what"?, and Brand and Jax (2007) question if there are "any possibilities to estimate or measure the resilience of an ecosystem". But can a definition of resilience really be purely descriptive as Brand and Jax (2007) demand in order to be a suitable concept for application within ecological science? The missing specifications of "identity", "structure and functions" and "basin of attraction" are inevitable as they strongly vary from ecosystem to ecosystem, depending on the spatial and temporal scale (Walker et al. 2002; Redman and Kinzig 2003), the system's boundaries, the hierarchical level, the variables of interest and many other factors. In other words, resilience, adaptability and vulnerability are always observer-dependent and therefore are always normative.

However, there is a necessity to clearly distinguish the ideas of resilience and adaptability in order to enhance conceptual clarity. We try to do this by including the concept of ecological integrity into the debate: *A system has a high adaptability if the sum of all disturbances and changes in the attractor domains do not reduce the system's degree of self-organization.*

In this definition, adaptability of an ecosystem refers to long-term changes and thus to a higher hierarchical level than resilience. Hence, the important property of a system with adaptive capacity is a trajectory that follows orientor dynamics, which is a general feature of ecosystem dynamics, but also a human target and therefore can become a normative property. In contrast, *resilience refers to the ability of a system to reorganize after a disturbance and remain in the previous basin of attraction*. Resilience does not correspond to a long-term trajectory of the attractor, but to the reaction after a single disturbance, excluding the dynamics on higher hierarchical levels.

6 Case Studies About Ecosystem Integrity and Resilience

To demonstrate the proposed interrelationship between integrity and the measures for ecosystem dynamics, two case studies will be sketched. Both cases are related to the development of wetland ecosystems. To summarize their basic features, the stability checklist from Gigon and Grimm (1997) has been applied in Table 4.

6.1 Case Study Wetland Retrogression

The first case study demonstrates disturbance dynamics in the wetlands of the Bornhöved Lake District in Northern Germany. Here a holistic indicator system, which has been developed on the base of orientor theory (see Table 1) has been used

Table 4 An application of the stability check list after Gigon and Grimm (1997). Following the authors, the methodological questions asked in this list have to be taken into account referring to any characterization of ecosystem dynamics. The data have been originally presented in Müller et al. (2006) and Schrautzer et al. (2007)

	Wet grassland retrogression	Wet grassland resilience
Which level of organization?	Ecosystem	Ecosystem
Which spatial scale?	Bornhöved lake district	Northern Germany
Which temporal scale?	~30 years development 30 years simulations	~100 years development 60 years simulations
Which disturbance?	Eutrophication Drainage	Deforestation Eutrophication Drainage Mowing Grazing
Which indicator in the ecosystem?	Ecosystem integrity indicator set	Ecosystem integrity indicator set (Table 1)
Which stability feature?	Change of single indicator values	Change of single indicator values
Which reference points or dynamics?	Mostly disturbed system	Maximum performance of single indicators
Which method of quantification?	Measurements and model runs	Measurements and model runs
Which normative aspects are taken into account?	Ecosystem approach	Ecosystem approach of the CBD

to demonstrate some steps of wetland retrogression as provoked by eutrophication and drainage. A comprehensive description of the study can be found in Müller et al. (2006).

On the base of field measurement, mappings and ecosystem classifications different wetland types have been analysed with the computer based digital landscape analysis system DILAMO (Reiche 1996) and the modelling system WASMOD-STOMOD (Reiche 1996) which was used to simulate the dynamics of water budgets, nutrient and carbon fluxes based on a 30 years series of daily data for meteorological and hydrological forcing functions. The model outputs were validated by measured data in representatives of these systems. The model results were extended to include data sets concerning ecosystem features by the integrity variables from Table 1.

The wet grasslands of the Bornhöved Lake District are exposed to the following management measures: drainage, fertilisation, grazing, and mowing in a steep gradient of ecosystem disturbances. The systems have been classified due to these external input regimes, and in Fig. 3 the sequential consequences of these disturbances can be seen in a synoptic manner: As the farmer's targets, the improvement of production and yield, are successfully fulfilled, the net primary production (NPP) is increasing by a factor of 10. Simultaneously the structural indicator (no. of plant species) is decreasing enormously throughout the retrogression. Also the efficiency

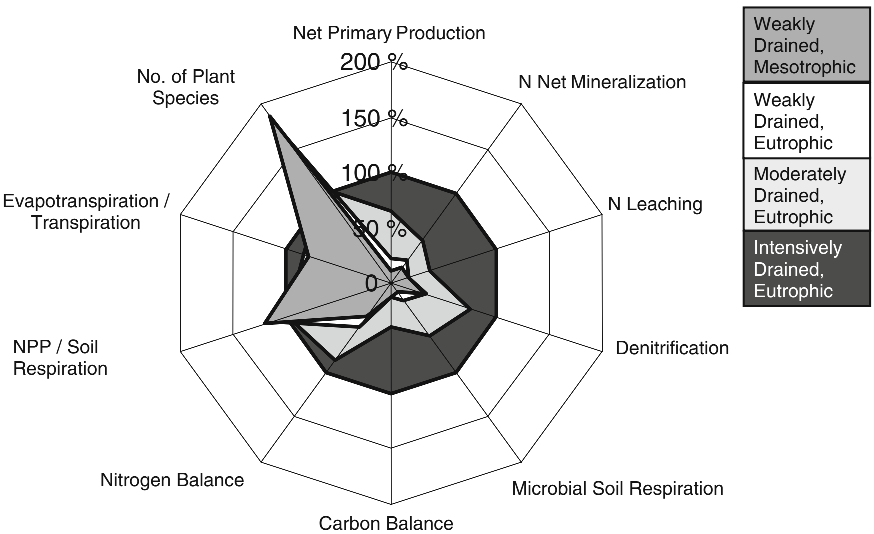

Fig. 3 Amoeba diagram representing indicators of ecosystem integrity during a retrogressive development in different wet grasslands of the Bornhöved Lake District. The values of the most degraded state have been set as 100%. The degradation has been mainly caused by different degrees of eutrophication and drainage. Starting with the initial state ("weakly drained, mesotrophic"), drainage and eutrophication of the wet grassland ecosystems affect irreversible changes up to the reference state "intensively drained, eutrophic". During that development ecosystem structures are reduced, energy and matter efficiencies decrease, and the originally sink function of the ecosystem turns into a source for nitrogen and carbon compounds. After Müller et al. (2006)

measures (NPP/soil respiration) are going down, and the biotic water flows (transpiration/evapotranspiration) get smaller. On the other hand, the development of the nitrogen and carbon balances demonstrates that the system is turning from a sink function into a source, the storage capacity is being reduced, and the loss of carbon and nitrogen compounds (all indicators on the right side of the figure) is rising enormously. Due to these dynamics we can state that there has been an enormous decrease of ecosystem integrity. As many of the processes are irreversible, the capacity for future self-organization is reduced to a very small degree.

If we now take a critical look at the resilience definitions and apply them on a small scale, it turns out that this variable behaves opposite to integrity: If this index is low, the potential for recovery is high, and also the necessary return time would be small. Thus, the higher the degradation of an ecosystem, the higher will be its resilience. Of course this context raises a further question for the resilience of the whole successional series: Is there a way back to a more integer ecosystem state after such a sequence of degradations?

6.2 Case Study Restoration Potential

In this second case study the scope of successional stages has been enhanced. The series leads from nature-near alder breaks to degraded wet pastures in 5 steps. The depiction in Fig. 4 is based on an intensive data sampling in wetlands all over Northern Germany, the interpretation of several ecological and botanical time series and on the thorough interpretation of successional studies in Northern German wetlands (see Schrautzer 2004). By model applications it was possible to quantify the indicator set of the retrogressional study. Therefore, the results which are illustrated in Fig. 4 allow for a wide range of interpretations, which will be restricted here to the basic elements of ecosystem integrity.

The amoeba diagrams in Fig. 4, which were used to summarize the outcomes of the investigation, once more represent the selected indicators that have been shown in Table 1. Their position can be found on the lower left side of the Figure. The reference values (100%) were chosen from the whole data set. They represent the highest value found for the respective variables. Negative values can be found with reference to the budgets of carbon and nitrogen, which in that cases function as landscape sinks. On the left hand sides of the amoeba diagrams those indicators are arranged which represent a high level of integrity with high values, while the parameters on the right sides of the amoeba demonstrate a loss of nutrients and gradients if their values are high. Consequently a qualitative estimation of the systems' integrity can be derived from the form of the amoeba value areas.

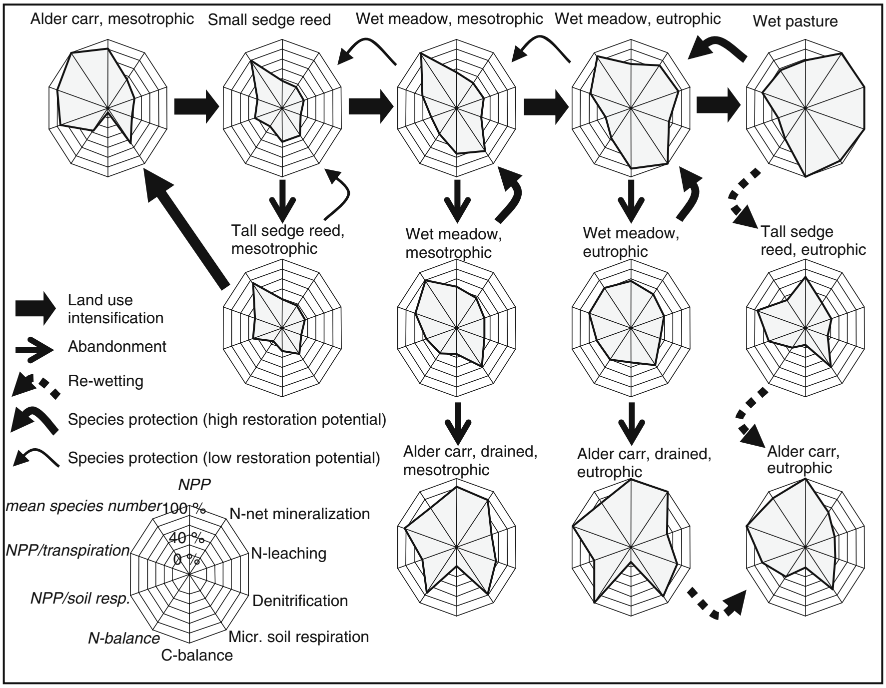

Fig. 4 Amoeba diagrams of sequential indicator values for ecosystem integrity during a retrogressive succession following land use intensification, and progressive successions following abandonment. The highest parameter values for all successional stages were set as 100%. Negative values concerning C- and N-balances represent a sink function of the systems. After Schrautzer et al. (2007)

The sequence of retrogressional states starts in the upper row of the Figure with the mesotrophic alder carr. Moving to the right (symbolized by the bold arrows), land use is intensified by deforestation, drainage, eutrophication, grazing and mowing, and in the end the state of a wet pasture is reached, which can be characterized by a low diversity, decreased ecological efficiencies and by a loss of nutrients, e.g., by high mineralization rates, high nitrate outputs by leaching, and high nitrogen loss through denitrification. Consequently these systems turn the landscape function of a nutrient and carbon sink into a source.

In contrast to the preceding case study, here also the question whether the changes are reversible or not has been posed to the data, and four different landscape management measures have been distinguished; abandonment, species protection measures with two different restoration potentials, and re-wetting. In Fig. 4 these modifications are symbolized by different arrows. The small straight arrows represent the consequences of abandonment, which could be perceived as a natural recovery measure. Thus, if a system is able to return to the starting formation, it would behave in a resilient manner. Studying the successional series, it becomes obvious that only in one case (alder carr → small sedge reed → tall sedge reed → alder carr) such dynamics are possible. Only in this case the original ecosystem can be restored. All other series of abandoned ecosystems lead to different ecosystem types: drained and mostly eutrophicated alder forests, which are depicted in the lower row of the figure. At a first glance, these systems look very similar to the initial state, but concerning the diversity, the metabolic efficiency, the N balances and the nitrogen loss, the indicator values indeed differ a lot from the starting state. As the systems are defined functionally, there is a decreased resilience in comparison with the only returning pathway. This context may be underlined if we use Pimm's measure of resilience: The successions which lead to the lower line of the figure need much longer times than the reversible one.

Additionally two results can be derived from the study: The species protection measures mostly enable a one-step-return only and they do not re-develop the initial stage. And even if extreme management activities like rewetting are carried out, the result will not be identical with the stating point, although the process takes a long time.

With reference to the discussion of ecosystem dynamics and resilience, this case study documents the high normative loading of all potential interpretations: The evaluation is a result of the observer's objectives, her or his indicators and the applied thresholds of reversibility, which are also defined by the observer:

If we return to the idea of attractor states to characterize resilience, the question is which width of the attractor basin is defined before a change of the system's regime is accepted. Are wetlands with alders healthy alder carrs? Or do we have to take into account their functionality as well?

The next normative point is the scale of observation: If we concentrate on the recovery potential of single states, the results might be satisfactory, because some of the species protection measures in fact are successful. If we choose the total retrogressional series, the result will be frustrating. Furthermore, the recovery potential of course also is a function of the selected time scales. And additionally also the potential investment into the treated wetlands is a parameter with important consequences for the evaluation.

The observer might also concentrate on a smaller amount of variables. The targets, results and the restorer's satisfaction might be very different if he or she wants to improve biodiversity or climate protection or ecosystem integrity.

Regrettably, one further consequence can be drawn: Degraded and "simple" ecosystems provide a much higher resilience than healthy ones (e.g., it might not be hard to restore a simple pioneer system but much effort and patience will be necessary for the restoration of a complex ecological entity), they have a much higher buffer capacity than complex systems, but the latter represent a high degree of ecosystem integrity.

In spite of the multitude of consequences and interpretations, the two wetland case studies hopefully could show that it is possible to indicate ecosystem integrity, thus to characterize the state of an ecosystem based on a concept of complexifying dynamics. And additionally it is also possible to depict resilience or adaptability on the base of ecosystem data and indicator sets.

7 Concluding Remarks

In this paper we have tried to discuss and illustrate some items of the actual debate about ecosystem dynamics. Returning to the initial objectives and questions of the article, some assertions can be formulated in the end. They are stated under the impression that stability of ecosystems is an accepted illusion, while dynamic development is a fact. Within this final discussion some aspects of this idea can be summarized, taking the initial questions of the paper as a guideline:

- *Is there a general tendency in undisturbed ecosystem development?*

In undisturbed ecosystem development there are different tendencies if we choose different scales of observation. Therefore, the consideration of constructive or destructive developmental phases is a function of the observer's objectives. For example, evolutionary investigations have to cope with all phases of the adaptive cycle, while the analysis of successions might lead to a preference of complexifying phases, and disturbance ecology will often concentrate on the consequences of the "release stage". Ecosystem theory has put emphasis on the phase of complexification, because nature-near ecosystems operate in a complexifying developmental trail for the longest time of their existence. Furthermore, a break down on a lower level of observation might be part of an adaptation process on a higher level that optimizes orientor values at a long-term scale.

Within these boundary conditions, general developmental trends of ecosystem features can be detected, understood and forecasted. When an ecosystem approaches the bifurcation point of Holling's release phase, its future fate can not be foreseen.

- *How can this trend be indicated?*

During the complexifying phase, orientors are optimized within the limits of the respective site conditions. These variables can be used as indicators to illuminate the state of the system. To describe an ecosystem in a holistic way, structural and functional attributes should be included, water, matter and energy budgets should be characterized and inputs, outputs, internal flows and efficiencies should be taken into account. These functional requirements are preferable demands for environmental applications: If an index with a higher degree of aggregation is selected (e.g., exergy storage, ascendancy or emergy), the overall results will also be visible, but it is hard to understand the functionality of disturbances and to derive respective management measures.

• *Which is the role of disturbance throughout ecosystem dynamics?*

In disturbed phases of development the orientor system and the ecosystem's hierarchical structure is broken. Functional modifications will lead to structural changes, and the system will approach a new state. If this state is situated within the old domain of attraction the system behaves resilient. If its position is outside the latitude (the width of the domain of attraction), a new steady state will be approached. The magnitude of the disturbance will influence the longer-term consequences and resilience as well as adaptability. Destruction and decay can be understood as "normal" components of natural development, and consequently – in an attitude towards nature conservation which still lacks a theory-based discussion – they could also be seen as basic processes supporting long-term innovation and adaptation.

• *What are the recent comprehensions within the resilience and adaptability concept?*

In the literature several features characterizing ecosystem dynamics can be found: e.g., stability, resistance, resilience, buffer capacity, elasticity, adaptability on the "stable" side and vulnerability, fragility, transformability to describe the conditions of the receptors. As a result of the preceding discussion of these terms, two focal comprehensions are proposed as guiding indicators of ecosystem dynamics: A system has a high adaptability if the sum of all disturbances and changes in the attractor domains do not reduce the system's degree of self-organization.

Resilience refers to the ability of a system to reorganize after a disturbance and remain in the previous basin of attraction. The difference between these concepts arises from the scale of observation: While adaptability considers longer developmental durations and attractor dynamics, resilience should be used for short time investigations, when the attractor composition does not change noticeably.

Resilience and integrity can not be linked directly. The respective investigations demonstrate that the higher an ecosystem's complexity and integrity is, the smaller is its resilience. Therefore the two conceptions seem to be counter moving; simple ecosystems provide a high resilience while systems with a high integrity have a low resilience. Consequently, they are more vulnerable with reference to disturbances. In contrast, adaptability in this comprehension can be directly related to integrity because orientor dynamics are taken into account by the inclusion of self-organized processes.

- *Is there a potential to quantify these attributes?*

The case studies have shown that an indication of the dynamic variables is possible. In the presented cases the resilience of the integrity variables has been characterized. These studies can also be used to demonstrate the demands and challenges for future work.

A focal problem arises from the *normative loading* of the resilience and adaptability concepts. This problem is not new. For example Picket and White (1985) have used a structural approach to define disturbance as *any relatively discrete event in space and time that disrupts ecosystem, community, or population structure and changes resources, substrates, or the physical environment*. The arising question referring to this definition is: how to denote the "normal state" of an ecosystem as a reference state with regard to disturbed states (Jentsch and White 2001)? Applying this problem to the resilience concept, similar questions would be:

- What is a regime of system states?
- Which are the thresholds of such a regime?
- How to define a regime shift?
- What is the function of the ecosystem?
- Which are the thresholds of the system's identity?

Actually there are no objective criteria to answer those queries. The observer defines his or her system, and the change of a system's resilience is one of the points which are defined case by case, lacking a scientific generalisation.

Finally, the question arises, which of the two above defined concepts will have a higher significance in the future. The difference is that resilience still considers the return to a former state, may be with a higher tolerance, than the stability concept, referring to a greater state space. Adaptability, following the proposed definition describes the ability of an ecosystem to return to an orientor trajectory. Thus, this concept is much more related to long-term developments on the one hand, and to the dynamic nature of the system's constraints on the other. Therefore, it might be very helpful in the context of the multiple changes we are facing. For example global climate change will modify the ecosystemic constraints drastically, making it impossible to return to the former situation in several instances. Thus, a search for the optimal conditions for adaptability might be much more helpful than resisting on a stability related resilient development, which might support systems that could become extremely dependent on external, protecting inputs of energy and work. The respective discussions and the development of adapted targets for ecosystem dynamics is an important task. It will be helpful to consider some ecosystem theoretical arguments within this process to find a balanced societal consensus.

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