Disturbance and stress - different meanings in ecological dynamics?

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Abstract

There is an increasing frequency of papers addressing disturbance and stress in ecology without clear delimitation of their meaning. Some authors use the terms disturbance and stress exclusively as impacts, while others use them for the entire process, including both causes and effects. In some studies, the disturbance is considered as a result of a temporary impact, which is positive for the ecosystem, while stress is a negative, debilitating impact. By developing and testing simple theoretical models, the authors propose to differentiate disturbance and stress by frequency. If the frequency of the event enables the variable to reach a dynamic equilibrium which might be exhibited without this event, then the event (plus its responses) is a disturbance for the system. If frequency prevents the variable's return to similar pre-event dynamics and drives or shifts it to a new trajectory, then we are facing stress. The authors propose that changes triggered by the given stimuli can be evaluated on an absolute scale, therefore, direction of change of the variable must not be used to choose one term or the other, i.e. to choose between stress and disturbance.

Introduction

Ecosystems are changing throughout time. However, depending on the scale of observation, they may show characteristics that correspond to a relatively stable, equilibrium state (Wiens, 1989). Equilibrium states are vulnerable: they might change abruptly or gradually due to repetitively, stochastically or continuously acting events.

Disturbance, perturbation and stress are the terms that denote to these events in ecological studies. Application of the term disturbance goes back as far as the beginning of the last century (Cooper, 1926). The term perturbation has also been used since the early ages of ecology as synonym of disturbance (Rykiel, 1985). After Selye (1936) published the physiological stress concept, it became popular in other fields of science, e.g. psychology

(Lazarus, 1966) sociology (Baker & Chapmen, 1962), or ecology (Barrett, 1968; Esch et al., 1975). Based on the Web of Knowledge (ISI) database, the term disturbance occurred 144 times in the title of articles between 2000 and 2005, while 1245 times between 2006 and 2011. The occurrences of the term stress were 89 and 153 for these periods. Despite the increasing number of papers addressing disturbance and stress in ecology, the use of these terms remained ambiguous. In the scientific literature "disturbance" generally refers to an important factor affecting community structure and dynamics (Pickett and White, 1989) preventing its self-organization towards an ecological equilibrium (Reynolds et al., 1993). Many authors use this term for destructive events, e.g. storms (Connell, 1978), floods (Biggs, 1995), fire or insect outbreaks (Johnson, 1992).

The use of the term stress is much less consistent across studies. Definitions depend on the background of the researchers and the research objects (Otte, 2001). The terminological inconsistency is clearly illustrated by the following stress definitions:

-„perturbation (stressor) applied to a system" (Barrett et al., 1976);

- „stress, consists of factors that place prior restrictions on plant production" (Grime, 1979);

- "unfavorable deflections" (Odum et al., 1979);

- „detrimental or disorganizing influence" (Odum, 1985);

- „external force or factor, or stimulus that causes changes in the ecosystem,"(Rapport et al., 1985);

-"external constraints limiting the rates of resource acquisition, growth or reproduction of organisms" (Grime, 1989);

-"Any environmental factor which restricts growth and reproduction of an organism or population'' (Crawford, 1989);

- „exposure to extraordinarily unfavourable conditions'' (Larcher, 1991),

-„environmental influences that cause measurable ecological changes" (Freedman, 1995);

-"conditions that cause an aberrant change in physiological processes resulting eventually in injury" (Nilsen and Orcutt, 1996).

-"Stress is evoked in organisms living at the edges of their ecological niches, where environmental conditions may exceed the ranges required for normal growth and development." (Roelofs, 2008).

Reading these examples it can be concluded that there is no clear difference between definitions used for disturbance and stress and attempts at discrimination of these terms are rare (Stenger-Kovács et al., 2013). An additional difficulty is that some authors use the terms disturbance and stress exclusively as stimuli, while others use them for the entire process, including both causes and effects. In some studies, the disturbance is considered as temporary setback, which is positive for the ecosystem, while stress is a negative, debilitating impact (Rapport & Whitford, 1999). What is common in the definitions can be summarised as follows: due to some (external or internal) stimulus one (or several) of the system attributes change(s) considerably. Rykiel (1985) overviewed the semantic and conceptual problems of the terms and made a proposal for working definitions of perturbations, stress and disturbance, but these did not become generally accepted. (Partly, because his concept did not fit into other models, e.g. Grime's well-known CSR theory).

The lack of consensus on definitions leads to semantic confusion and conceptual ambiguity, which results in difficulties in finding connections between various models used in ecology.

The aim of this study is to propose model-based definitions for stress and disturbance.

Theory

Our definitions rest upon four basic principles. First, both terms (stress and disturbance) imply the whole process, that is, the impact, the system impacted and response of the system. The second, direction of the changes in the system attributes is irrelevant. The third, frequency of the impact is of basic importance. The fourth, we supposed that in equilibrium state the system attribute remains constant.

The above principles serve as a basis for distinguishing disturbance and stress. Supposing that the impact is decisive, behaviour of the ecosystem can be represented in an x-y plane, where x-axis corresponds to time, while y-axis corresponds to an arbitrary system attribute (Fig. 1).

Ideally, we suppose that the ecosystem is in an equilibrium state when the given state variable statistically does not change through time. As a result of an impact, the value of the system attribute changes (into positive or negative directions) and this is followed by recovery and return to unimpacted state. Time needed for the system to reach the basic level is defined as recovery time (RT later in the text) (Fig. 1.).

If the frequency of the stimulus increases (Fig. 2b-c) (i.e. the time between the periodic events < RT), the system variable sets back prior to complete recovery.

Frequently occurring events result in early setbacks, thus the system performs like those that are under the pressure of a continuously active agent (Fig. 2c).

Based on the possible scenarios shown above, disturbance is defined as occasionally occurring or periodic event (when the time between events >RT) that results in an abrupt change of the system, with the possibility of recovery (Fig. 2a).

Stress is defined as frequently occurring (time between events <RT) or continuous event, when as a result of the impact the system does not recover, therefore, value of the system variable does not reach the basic level (Fig. 2b, c).

Integration of the terms in ecological models

When new definitions are proposed it is worth elucidating their relationship with existing models and phrasings. In case of the CSR theory (Grime, 1974), which is developed to classify adaptive strategies in terrestrial plant species, stress is defined as „external constraints limiting the rates of resource acquisition, growth or reproduction of organisms" (Grime, 1989). Based on this criterion, nutrients, water and heat are considered as stressors. In most of the cases these resources act continuously on macrophytes, therefore, based on our proposed definitions, these are also stressors. But Grime's definitions cannot be applied to well known phenomenon like eutrophication, since the nutrient enrichment increases the rate reproduction and growth of plants. Thus, we argue that Grime's stress definition cannot be considered as generally accepted approach, which can be applied for all situations. In our opinion none of the environmental constraints can be declared as stressor or disturbance-creating impact without considering the frequency of the impact and resilience of the recipient system. As to the intermediate hypothesis (IDH), based on our definitions both high and intermediate disturbances are considered as stress event for the system because frequency of the impact does not allow the system to reach the low diversity state which should ensue from the Hardin's competitive exclusion theory (Hardin, G. 1961).

Analysis of shallow lakes' phytoplankton time series records serve as an example for both disturbance and stress events. Padisák (1993) demonstrated that wind induced disturbances of intermediate frequency (~3-5×generation time) resulted in characteristic periodic changes in phytoplankton diversity in Lake Balaton, while at low disturbance frequency diversity diminished. Wind induced mixing of high frequency (~ daily) in the large, very shallow Neusiedlersee rolls back euplanktic taxa and contributes to the development of a unique meroplankton dynamics (Padisák & Dokulil, 1994), during which large size diatoms of benthic origin predominate in the turbid water. These examples demonstrate that different frequencies of otherwise identical influences lead to different responses. Based on the reasonings of the previous paragraph, low disturbance events at Lake Balaton are typical disturbances, while events of intermediate and high frequency are considered as stress for the lake's phytoplankton.

Occasionally both disturbance and stress might have serious or fatal consequences. Fig. 3 illustrates the situation where the measure of the stimulus (and the system response) is constant. In case of stress the value of the system variable decreases step by step, does not stabilise at a certain level and finally reaches the Y=0 value. (This process is responsible for the extinction of sensitive taxa during pollution).

Fatal disturbances can also develop when complete recovery of the system cannot be accomplished. The process is similar to that shown in Fig. 2a, but needs a reasonably longer period of time. This process can be observed in nature when periodic floods wash out species from pools or streambeds (Fig. 4).

In the examples shown above the impacts were physical processes, while diversity was used as response variable. Nevertheless disturbance and stress can be induced by various other agents and both subsume a variety of ecological manifestations. Rapport and Whitford (1999) classified the impacts into four main groups: physical restructuring; discharge of waste residuals; introduction of exotic species; and overharvesting. That the given impact results in a disturbance or stress cannot be prognosticated without the knowledge of the temporal and spatial characteristics of the stimulus and characteristics of the ecosystem affected. For example, recurrent floods (Fig. 5a) are perceived as stress for fish (Fig. 5b) and are perceived as disturbance for benthic algae (Fig. 5c).

Adaptations

Changes of the environment evoke adaptational responses at various timescales and at different levels of biological organisation. Frequency of changes of the environment basically influences the level of response. Continuous and high frequency impacts might generate physiological, population-level and community-level adaptational mechanisms. Adaptation of phytoplankton to low incident light intensity serves as an example for multi-level adaptation. Microalgae are capable of adapting to reduced photon flux densities individually by increasing the cellular pigment content or changing the pigment composition (Richardson et al., 1983). In low light conditions the selection acts continuously upon functionally related traits, favouring those, which utilize the light most efficiently within the population.

Community level adaptation is manifested as a change in species composition favouring algae that are capable for chromatic adaptation and/or have elongated form; therefore, considered as strong light competitors (Reynolds, 2006).

Adaptational responses require that individuals and populations be exposed to changes for a longer period of time; therefore, individuals or populations cannot adapt to abrupt events like disturbances. Nevertheless fatal disturbance might select the most sensitive taxa, but this process takes place at higher levels of organisation (community and ecosystem level) and operates at longer (evolutionary) time scale. These kinds of disturbances e.g. huge fish kills (Borics et al., 2000), storms (Scheffer, 1998) frequently occur in nature and are responsible for shifting of ecosystems between alternative stable states (Beisner et al., 2003).

After the organisms or populations adapted to the new conditions, these conditions cannot be regarded as stressful anymore (Otte, 2001) In this case the lack of the continuously acting impact means disturbance or stress for the system. Chorus (2003) demonstrated that in continuously mixed lakes the intermittent calm phases would represent a disturbance for the phytoplankton adapted to turbid conditions. She applied the term "intermediate quiescence" for this kind of situation.

It is important to note here that a number of simplifications were applied during development of the above models. For example, we disregarded that disturbances are in principle stochastic, unpredictable events (c.f. Reynolds et al., 1993), or that in lack of disturbance competitive exclusion will occur that, itself, results in change of the level of the system attribute (for example, diversity decreases; c.f. Connell, 1978). Furthermore, though it is inevitably important, we did not consider effects of intensity of impacts. These considerations can be incorporated into more complex models.

Conclusions

We proposed here to differentiate the terms disturbance and stress by their frequency. If the frequency of the event enables the variable to reach a dynamic equilibrium which might be exhibited without this event, then the event (plus its responses) is considered as disturbance for the system. If frequency prevents the variable's return to similar pre-event dynamics and drives or shift it to a new trajectory, then the event considered as stress. Thus, the use of the terms depends on the relationship between the frequency of the impact and resilience of the system variable.

The authors think that changes triggered by the given impact can be evaluated on an absolute scale. From terminological point of view there should not be good or bad changes, just changes. Thus, subjective judgement of ecosystems' changes (e.g. good or bad) should be avoided when disturbance and stress are defined.

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Legends for figures

Fig. 1.

Changes of an optional system variable (y) through time (x). Arrows indicate stimuli.

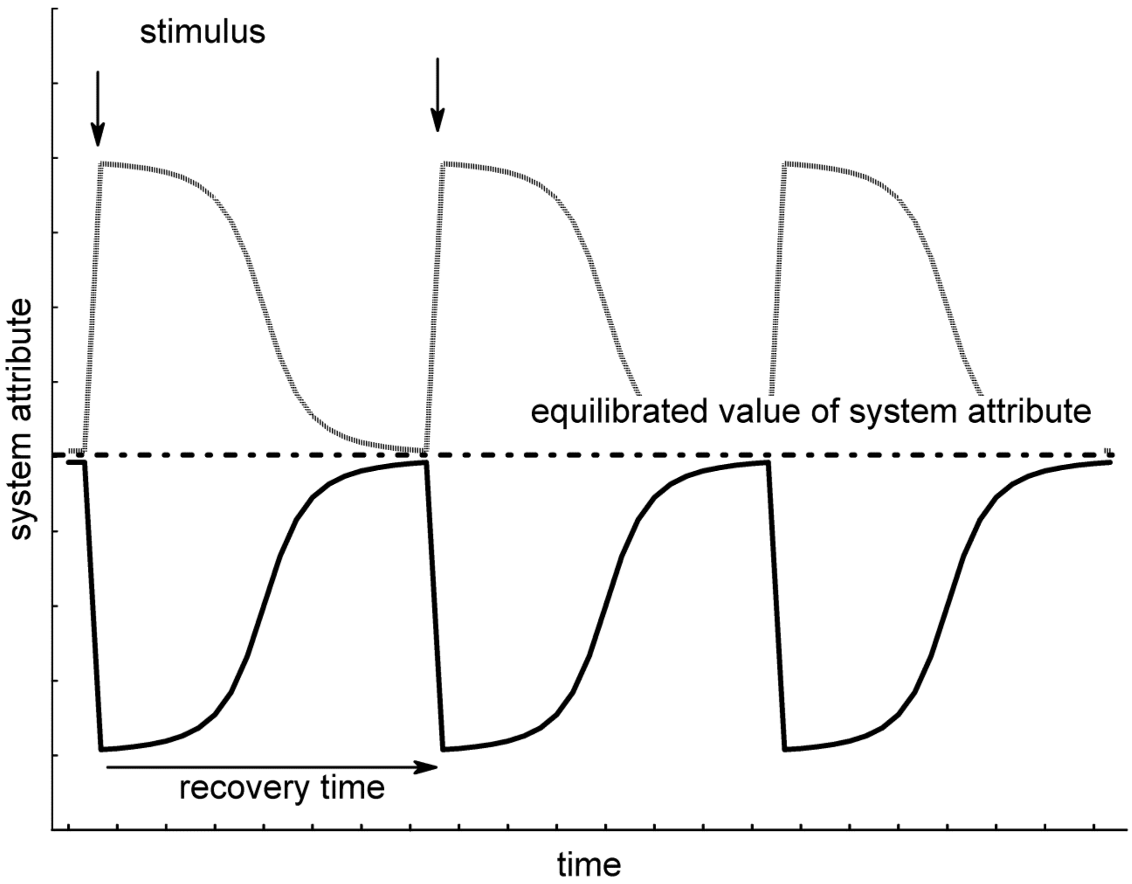


Fig. 2.

Changes of an optional system variable (y) through time (x) at low (a), at medium (b) and at high frequency stimuli (c).

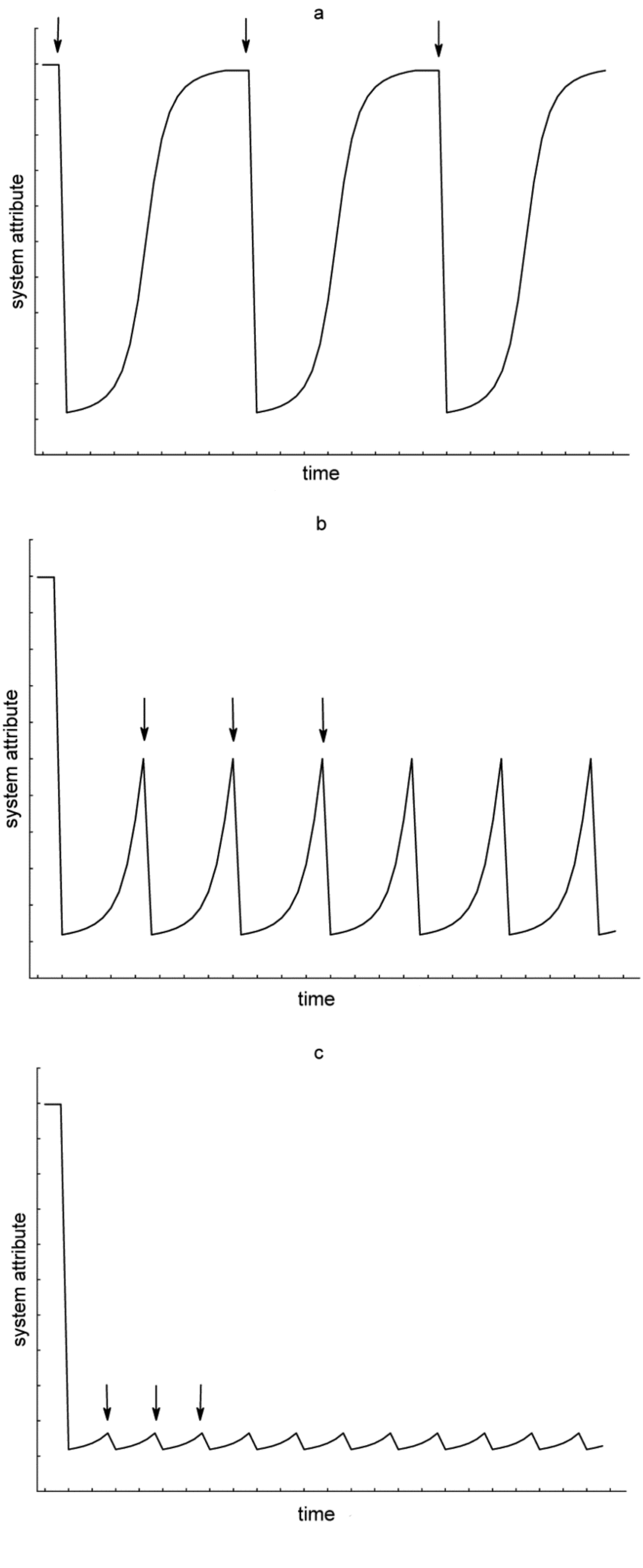

a
system attribute
time
b
system attribute
time
c
system attribute
time

Fig. 3.

Changes of a system variable (calculating with a constant setback) leads to stress of fatal consequences.

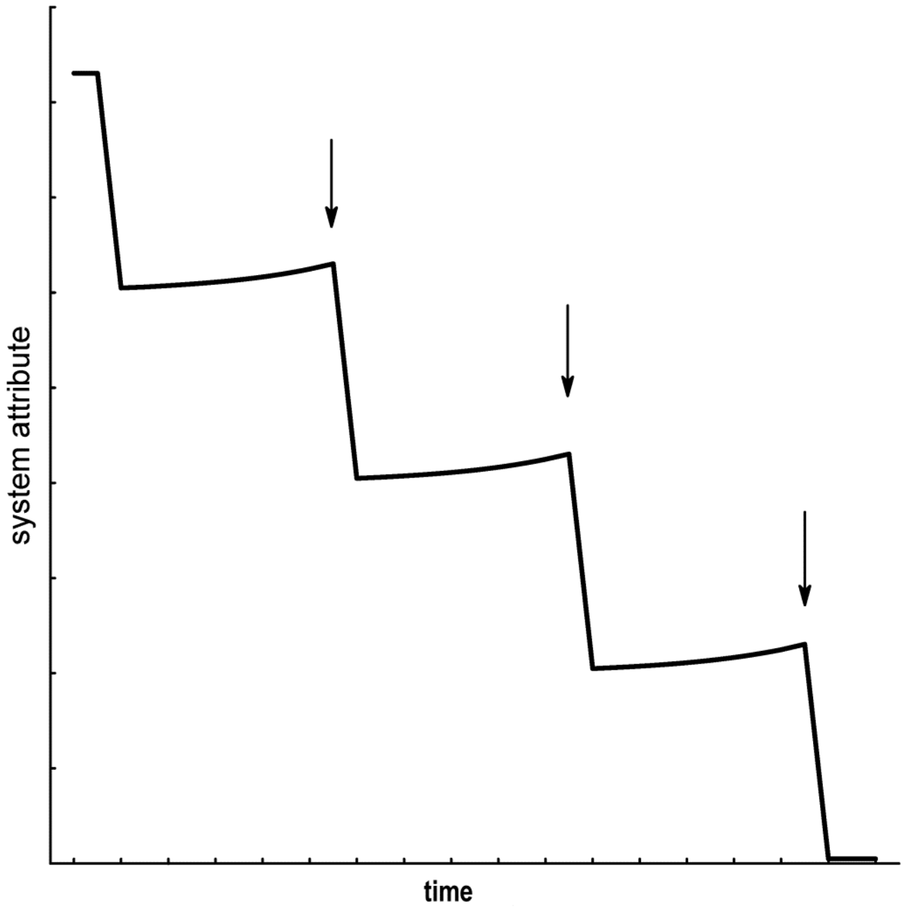


Fig 4.

Changes of a system variable (calculating with a constant setback) results in fatal disturbance.

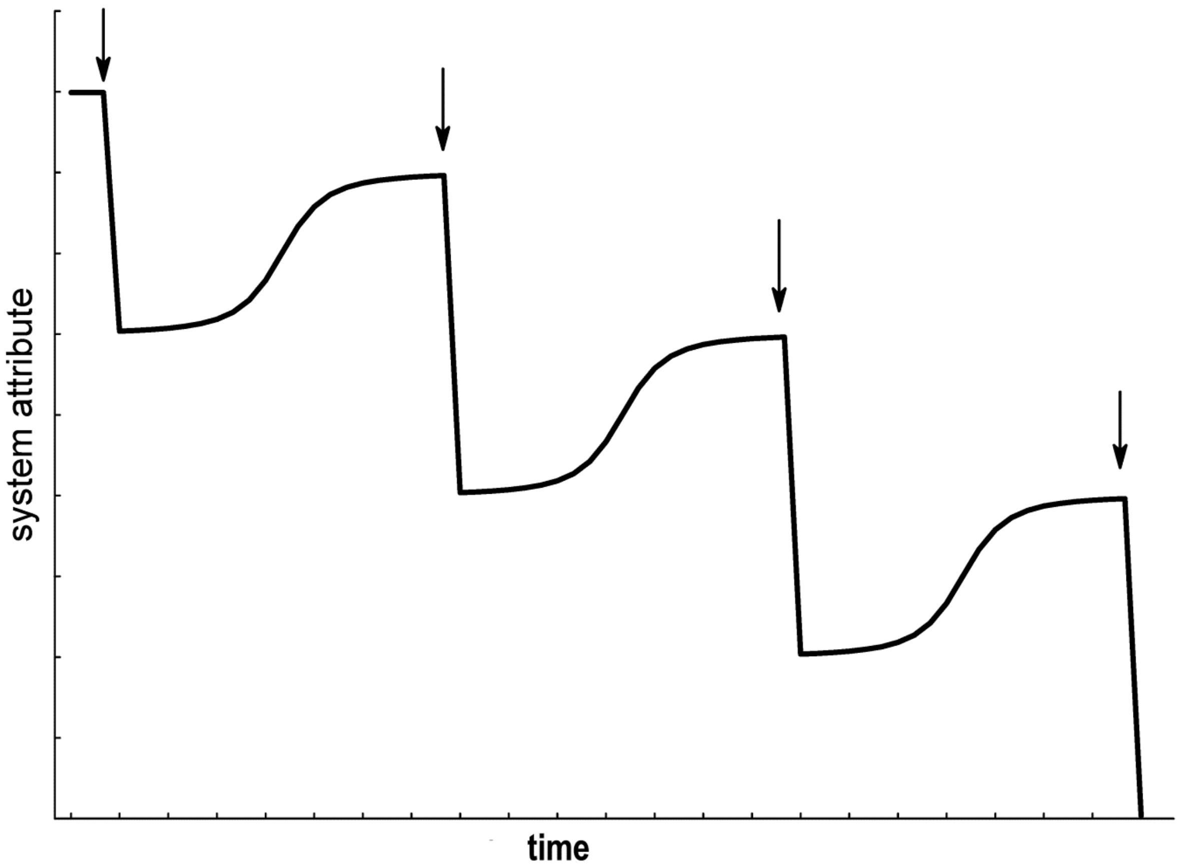
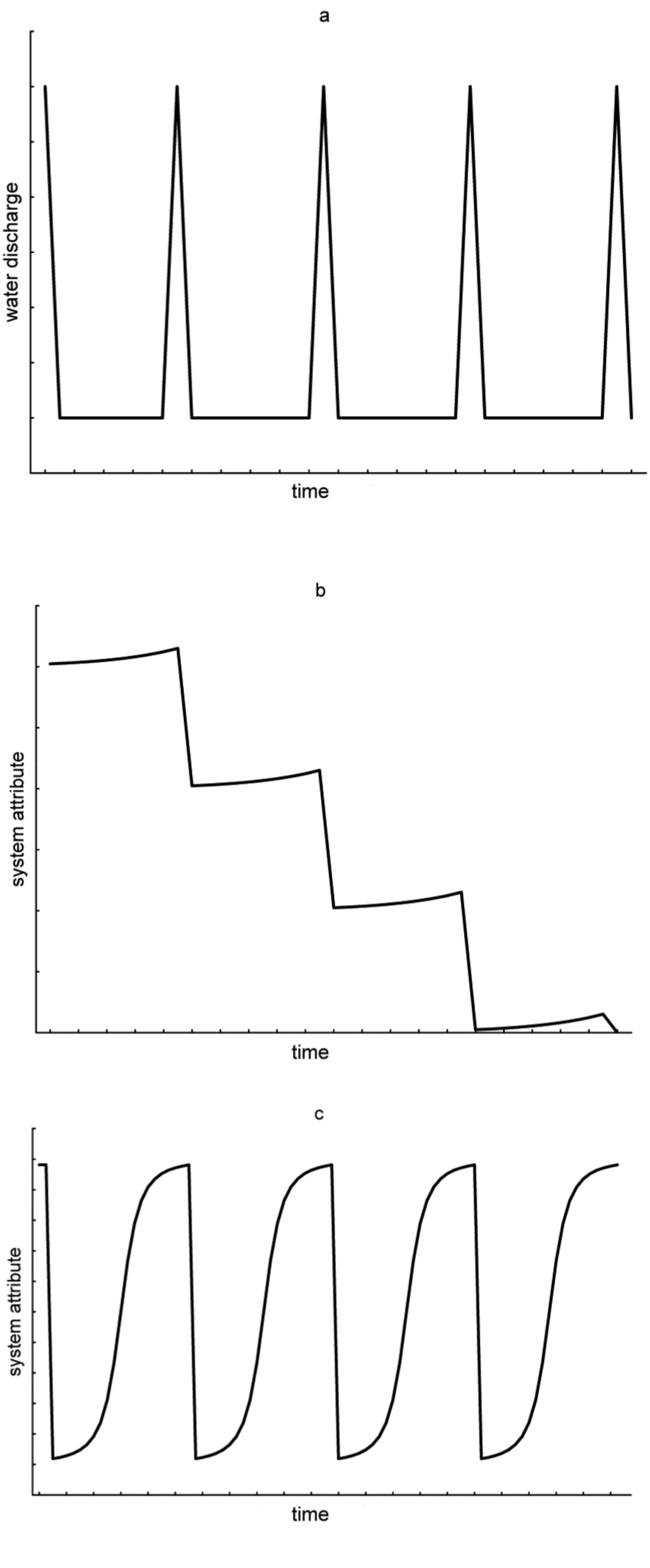


Fig. 5.

Impact of flood events (a) on different communities. Community needs longer (b) and shorter (c) recovery time.


a
water discharge
time
b
system attribute
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c
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time