Springer

Dear Author,

Here are the proofs of your article.

- You can submit your corrections **online**, via **e-mail** or by **fax**.
- For **online** submission please insert your corrections in the online correction form. Always indicate the line number to which the correction refers.
- You can also insert your corrections in the proof PDF and **email** the annotated PDF.
- For fax submission, please ensure that your corrections are clearly legible. Use a fine black pen and write the correction in the margin, not too close to the edge of the page.
- Remember to note the **journal title**, **article number**, and **your name** when sending your response via e-mail or fax.
- **Check** the metadata sheet to make sure that the header information, especially author names and the corresponding affiliations are correctly shown.
- **Check** the questions that may have arisen during copy editing and insert your answers/ corrections.
- **Check** that the text is complete and that all figures, tables and their legends are included. Also check the accuracy of special characters, equations, and electronic supplementary material if applicable. If necessary refer to the *Edited manuscript*.
- The publication of inaccurate data such as dosages and units can have serious consequences. Please take particular care that all such details are correct.
- Please **do not** make changes that involve only matters of style. We have generally introduced forms that follow the journal's style.
  Substantial changes in content, e.g., new results, corrected values, title and authorship are not allowed without the approval of the responsible editor. In such a case, please contact the Editorial Office and return his/her consent together with the proof.
- If we do not receive your corrections **within 48 hours**, we will send you a reminder.
- Your article will be published **Online First** approximately one week after receipt of your corrected proofs. This is the **official first publication** citable with the DOI. **Further changes are, therefore, not possible.**
- The **printed version** will follow in a forthcoming issue.

Please note

After online publication, subscribers (personal/institutional) to this journal will have access to the complete article via the DOI using the URL: http://dx.doi.org/[DOI].
If you would like to know when your article has been published online, take advantage of our free alert service. For registration and further information go to: http://www.springerlink.com.

Due to the electronic nature of the procedure, the manuscript and the original figures will only be returned to you on special request. When you return your corrections, please inform us if you would like to have these documents returned.

Metadata of the article that will be visualized in OnlineFirst

ArticleTitle	Disturbance and stress: different meanings in ecological dynamics?	
Article Sub-Title		
Article CopyRight	Springer Science+Business Media Dordrecht (This will be the copyright line in the final PDF)	
Journal Name	Hydrobiologia	
Corresponding Author	Family Name	**Várbíró**
	Particle	
	Given Name	**Gábor**
	Suffix	
	Division	Department of Tisza River Research, Centre for Ecological Research
	Organization	Hungarian Academy of Sciences
	Address	18/c. Bem Square, Debrecen, 4026, Hungary
	Email	varbirog@gmail.com
Author	Family Name	**Borics**
	Particle	
	Given Name	**Gábor**
	Suffix	
	Division	Department of Tisza River Research, Centre for Ecological Research
	Organization	Hungarian Academy of Sciences
	Address	18/c. Bem Square, Debrecen, 4026, Hungary
	Email	
Author	Family Name	**Padisák**
	Particle	
	Given Name	**Judit**
	Suffix	
	Division	Department of Limnology
	Organization	University of Pannonia
	Address	10. Egyetem str, Veszprém, 8200, Hungary
	Email	

	Received	7 December 2012
Schedule	Revised	11 February 2013
	Accepted	16 February 2013

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.

Keywords (separated by '-') Terminology - Frequency scale - Disturbance - Perturbation - Stress

Footnote Information Handling editor: Luigi Naselli-Flores

Journal: 10750
Article: 1478

Author Query Form

Please ensure you fill out your response to the queries raised below and return this form along with your corrections

Dear Author

During the process of typesetting your article, the following queries have arisen. Please check your typeset proof carefully against the queries listed below and mark the necessary changes either directly on the proof/online grid or in the 'Author's response' area provided below

Query	Details required	Author's response
1.	References Chorus and Schlag (1993), Hereford (2009), and Pickett and White (1985) are given in list but not cited in text. Please cite in text or delete from list.	
2.	Please check and confirm that the authors and their respective affiliations have been correctly identified and amend if necessary.	
3.	References Borics et al. (2000) and Chorus (2003) are cited in text but not	

	provided in the reference list. Please provide references in the list or delete these citations.	

Hydrobiologia
DOI 10.1007/s10750-013-1478-9

OPINION PAPER

Disturbance and stress: different meanings in ecological dynamics?

Gábor Borics · Gábor Várbíró · Judit Padisák

Received: 7 December 2012 / Revised: 11 February 2013 / Accepted: 16 February 2013

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.

Keywords Terminology · Frequency scale · Disturbance · Perturbation · Stress

Handling editor: Luigi Naselli-Flores

G. Borics · G. Várbíró (✉)
Department of Tisza River Research,
Centre for Ecological Research, Hungarian Academy of Sciences, 18/c. Bem Square, Debrecen 4026, Hungary
e-mail: varbirog@gmail.com

J. Padisák
Department of Limnology, University of Pannonia,
10. Egyetem str, Veszprém 8200, Hungary

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 & Chapman, 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 1,245 times between 2006 and 2011. The occurrences

Journal : Medium 10750 | Dispatch : 25-2-2013 | Pages : 7
Article No. : 1478 | □ LE | □ TYPESET
MS Code : HYDR-D-12-08202 | ✔ CP | ✔ DISK

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 et al., 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 & 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 et al., 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

Journal : Medium 10750 Dispatch : 25-2-2013 Pages : 7
Article No. : 1478 ☐ LE ☐ TYPESET
MS Code : HYDR-D-12-08202 ☑ CP ☑ DISK

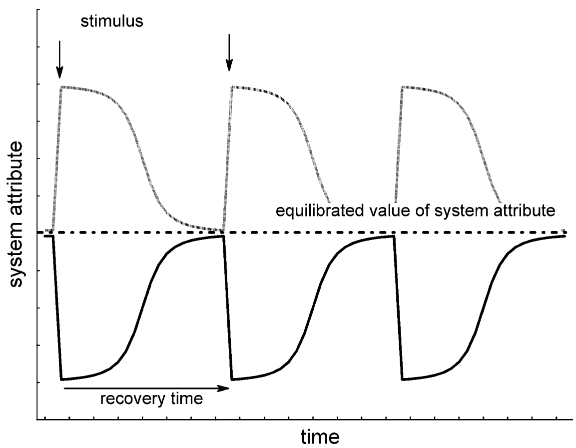

Fig. 1 Changes of an optional system variable (*y*) through time (*x*). *Arrows* indicate stimuli

events < RT), the system variable sets back before 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

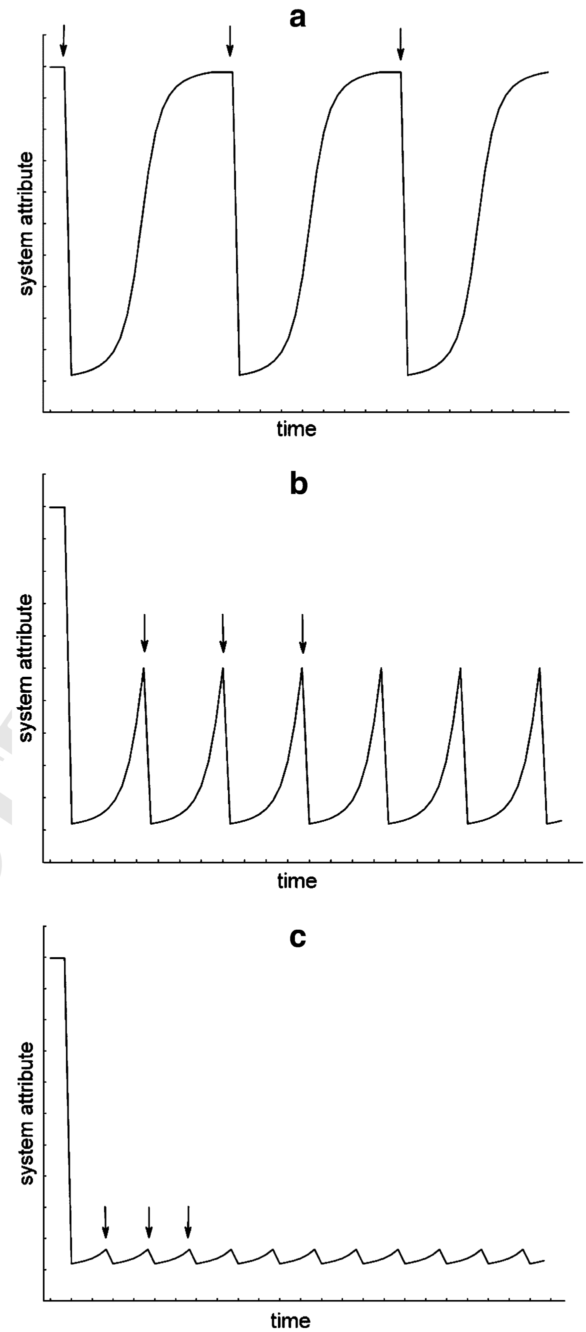

Fig. 2 Changes of an optional system variable (*y*) through time (*x*) at low (**a**), at medium (**b**) and at high frequency stimuli (**c**)

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

Journal : Medium 10750 | Dispatch : 25-2-2013 | Pages : 7
Article No. : 1478 | □ LE | □ TYPESET
MS Code : HYDR-D-12-08202 | ✔ CP | ✔ DISK

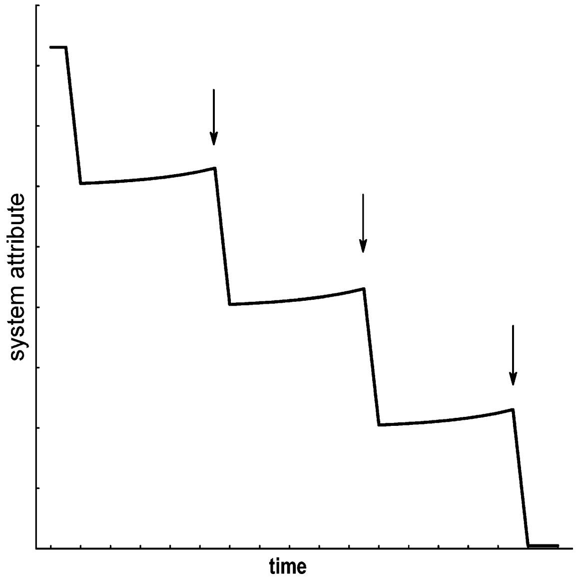

Fig. 3 Changes of a system variable (calculating with a constant setback) leads to stress of fatal consequences

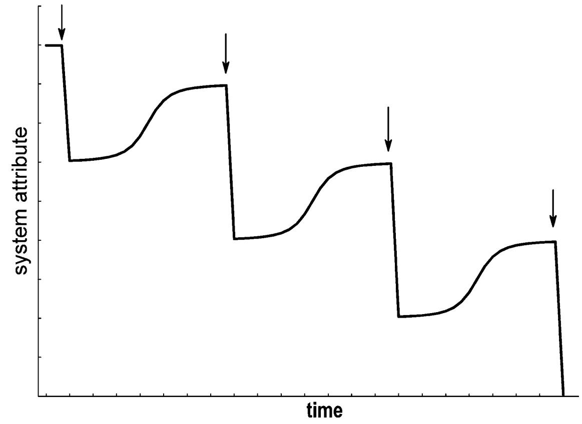

Fig. 4 Changes of a system variable (calculating with a constant setback) results in fatal disturbance

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, 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. Figure 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 & 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).

Journal : Medium 10750 | Dispatch : 25-2-2013 | Pages : 7
Article No. : 1478 | ☐ LE | ☐ TYPESET
MS Code : HYDR-D-12-08202 | ✔ CP | ✔ DISK

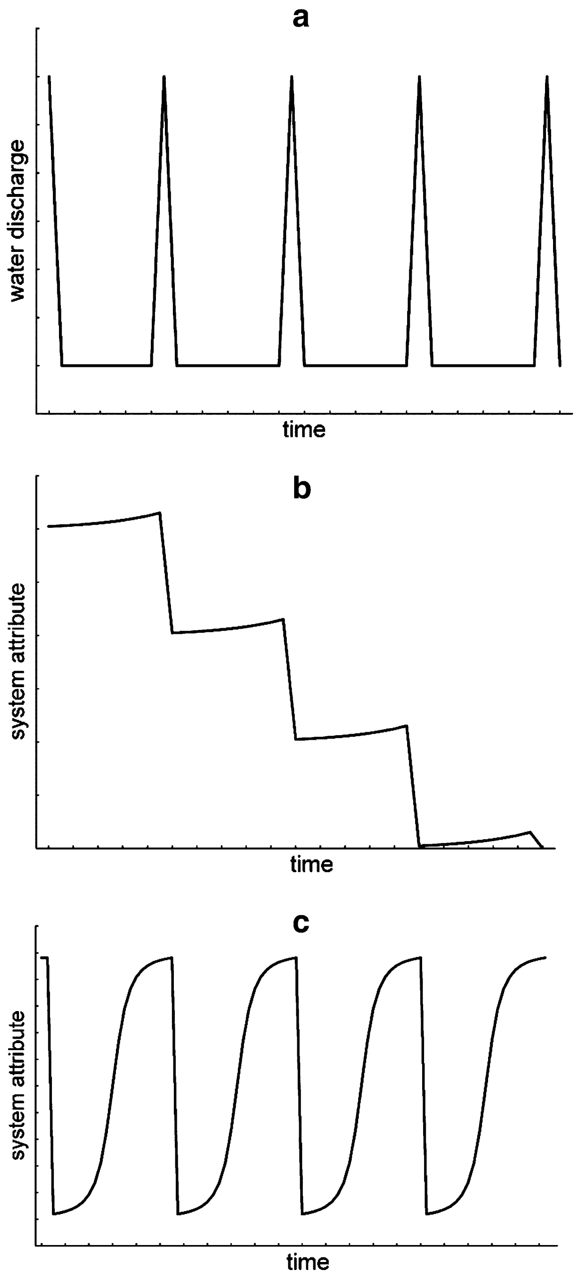

Fig. 5 Impact of flood events **a** on different communities. Community needs longer (**b**) and shorter (**c**) recovery time

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.

Journal : Medium 10750 | Dispatch : 25-2-2013 | Pages : 7
Article No. : 1478 | ☐ LE | ☐ TYPESET
MS Code : HYDR-D-12-08202 | ✔ CP | ✔ DISK

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.

Acknowledgments This project was supported by the Hungarian National Science Foundation (OTKA Nr. K 75552 and OTKA104279), Bolyai Fellowship of the Hungarian Academy of Science and the EU Societal Renewal Operative Program (TÁMOP-4.2.2.A-11/1/KONV-2012-0064).

References

Baker, G. W. & D. W. Chapman (eds), 1962. Man and Society in Disaster. Basic Books, New York.

Barrett, G. W., 1968. The effects of an acute insecticide stress on a semi-enclosed grass-land ecosystem. Ecology 49(6): 1019–1035.

Barrett, G. W., G. M. Van Dyne & E. P. Odum, 1976. Stress ecology. BioScience 26: 192–194.

Beisner, B. E., D. T. Haydon & K. Cuddington, 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1: 376–382.

Biggs, B. J. F., 1995. The contribution of flood disturbance, catchment geology and land use to the habitat template of periphyton in stream ecosystems. Freshwater Biology 33: 419–438.

Chorus, I. & G. Schlag, 1993. Importance of intermediate disturbances for species composition and diversity of phytoplankton in two very different Berlin lakes. Hydrobiologia 249: 61–92.

Connell, J., 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1304–1310.

Cooper, W. S., 1926. The fundamentals of vegetation change. Ecology 7: 391–413.

Crawford, R. M. M., 1989. Studies in Plant Survival-Ecological Case Histories of Plant Adaptation to Adversity. Blackwell Scientific Publications, Boston: 296 pp.

Esch, G. W., J. W. Gibbons & J. E. Bourque, 1975. An analysis of the relationship between stress and parasitism. American Midland Naturalist 93: 339–353.

Freedman, B., 1995. Environmental Ecology—The Ecological Effects of Pollution, Disturbance, and other Stresses, 2nd ed. Academic Press, San Diego: 606 pp.

Grime, J. P., 1979. Plant Strategies and Vegetation Processes. Wiley, Chichester: 222 pp.

Grime, J. P., 1974. Vegetation classification by reference to strategies. Nature 250: 26–31.

Grime, J. P., 1989. The stress debate: symptom of impending synthesis? Biological Journal of the Linnean Society 37: 3–17.

Hardin, G., 1961. The competitive exclusion principle. Science 121: 1292–1297.

Hereford, J., 2009. A quantitative survey of local adaptation and fitness trade-offs. American Naturalist 173(5): 579–588.

Johnson, E. A., 1992. Fire and Vegetation Dynamics: Studies from the North American Boreal Forest. Cambridge University Press, Cambridge, UK: 144 pp.

Larcher, W., 1991. Physiological Plant Ecology, 2nd ed. Springer, Berlin.

Lazarus, R. S., 1966. Psychological Stress and the Coping Press. McGraw-Hill, New York: 466 pp.

Nilsen, E. T. & D. M. Orcutt, 1996. The Physiology of Plants Under Stress: Abiotic Factors. Wiley, New York: 689 pp.

Odum, E. P., 1985. Trends expected in stressed ecosystems. Bioscience 35: 419–422.

Odum, E. P., J. T. Finn & E. H. Franz, 1979. Perturbation theory and the subsidy-stress gradient. BioScience 29: 349–352.

Otte, M. L., 2001. What is stress to a wetland plant? Environmental and Experimental Botany 46: 195–202.

Padisák, J., 1993. The influence of different disturbance frequencies on the species richness, diversity and equitability of phytoplankton in shallow lakes. Hydrobiologia 249: 135–156.

Padisák, J. & M. Dokulil, 1994. Meroplankton dynamics in a saline, turbulent, turbid shallow lake (Neusiedlersee, Austria and Hungary). Hydrobiologia 289: 23–42.

Pickett, S. T. A. & P. S. White. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando: 472 pp.

Pickett, S. T. A., J. Kolasa, J. J. Armesto & S. L. Collins, 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54: 129–136.

Rapport, D. J. & W. G. Whitford, 1999. How ecosystems respond to stress. BioScience 49: 193–203.

Rapport, D. J., H. A. Regier & T. C. Hutchinson, 1985. Ecosystem behavior under stress. American Naturalist 125: 617–640.

Reynolds, C. S., 2006. Ecology of Phytoplankton. Cambridge University Press, Cambridge: 535 pp.

Reynolds, C. S., J. Padisák & U. Sommer, 1993. Intermediate disturbance in the ecology of phytoplankton and the maintenance of species diversity: a synthesis. Hydrobiologia 249: 183–188.

Richardson, K., J. Beardall & J. A. Raven, 1983. Adaptation of unicellular algae to irradiance: an analysis of strategies. New Phytologist 93: 157–191.

Roelofs, D., M. G. M. Aarts, H. Schat & N. M. van Straalen, 2008. Functional ecological genomics to demonstrate general and specific responses to abiotic stress. Functional Ecology 22: 8–18.

Rykiel, E. J., 1985. Towards a definition of ecological disturbance. Australian Journal of Ecology 10: 361–365.

Scheffer, M., 1998. Ecology of Shallow Lakes. Chapman and Hall, London: 357 pp.

Selye, H., 1936. A syndrome produced by diverse nocuous agents. Nature 138: 32 pp.

Stenger-Kovács, C., E. Lengyel, L. O. Crossetti, V. Üveges & J. Padisák, 2013. Diatom ecological guilds as indicators of temporally changing stressors and disturbances in the small Torna-stream, Hungary. Ecological Indicators 24: 138–147.

Wiens, J. A., 1989. Spatial scaling in ecology. Functional Ecology 3: 385–397.

Journal : **Medium 10750**	Dispatch : **25-2-2013**	Pages : **7**
Article No. : **1478**	☐ LE	☐ TYPESET
MS Code : **HYDR-D-12-08202**	☑ CP	☑ DISK