



Terms and Conditions of Use of Digitised Theses from Trinity College Library Dublin

Copyright statement

All material supplied by Trinity College Library is protected by copyright (under the Copyright and Related Rights Act, 2000 as amended) and other relevant Intellectual Property Rights. By accessing and using a Digitised Thesis from Trinity College Library you acknowledge that all Intellectual Property Rights in any Works supplied are the sole and exclusive property of the copyright and/or other IPR holder. Specific copyright holders may not be explicitly identified. Use of materials from other sources within a thesis should not be construed as a claim over them.

A non-exclusive, non-transferable licence is hereby granted to those using or reproducing, in whole or in part, the material for valid purposes, providing the copyright owners are acknowledged using the normal conventions. Where specific permission to use material is required, this is identified and such permission must be sought from the copyright holder or agency cited.

Liability statement

By using a Digitised Thesis, I accept that Trinity College Dublin bears no legal responsibility for the accuracy, legality or comprehensiveness of materials contained within the thesis, and that Trinity College Dublin accepts no liability for indirect, consequential, or incidental, damages or losses arising from use of the thesis for whatever reason. Information located in a thesis may be subject to specific use constraints, details of which may not be explicitly described. It is the responsibility of potential and actual users to be aware of such constraints and to abide by them. By making use of material from a digitised thesis, you accept these copyright and disclaimer provisions. Where it is brought to the attention of Trinity College Library that there may be a breach of copyright or other restraint, it is the policy to withdraw or take down access to a thesis while the issue is being resolved.

Access Agreement

By using a Digitised Thesis from Trinity College Library you are bound by the following Terms & Conditions. Please read them carefully.

I have read and I understand the following statement: All material supplied via a Digitised Thesis from Trinity College Library is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of a thesis is not permitted, except that material may be duplicated by you for your research use or for educational purposes in electronic or print form providing the copyright owners are acknowledged using the normal conventions. You must obtain permission for any other use. Electronic or print copies may not be offered, whether for sale or otherwise to anyone. This copy has been supplied on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

Defining disturbance in time: the ecological implications of varying temporal patterns of disturbances

Jorge García Molinos

B.Sc. (University of Valladolid, Spain)

M.Sc. (Napier University, Edinburgh, UK)



Thesis submitted in fulfilment for the degree of Doctor of Philosophy to the

University of Dublin, Trinity College

2010



phD Zoology

Declaration

I declare that this thesis is entirely my own work, except where otherwise stated, and that it has not previously been submitted to this or any other university. I give my permission to the library to lend or copy this thesis on request.



Jorge García Molinos



Thesis 9372

Summary

Prediction and mitigation of the effects of global environmental change rely primarily on our capacity to anticipate its causes and consequences. Key to this is the ability to identify and understand the mechanisms that cause and maintain those changes. Global change models frequently predict a general tendency towards increased temporal variability of disturbance regimes. It is not entirely clear, however, how such changes will affect the effects of disturbances on ecosystem processes. This thesis explores the importance of temporal properties of disturbances for regulating the responses of ecosystems to perturbations. I followed a mechanistic experimental approach to examine, through successive laboratory and field experiments, the contribution of different temporal properties to sediment disturbance effects on stream benthic assemblages. Importantly, my experimental designs allowed me to unconfound temporal cause and effect relationships from those of other disturbance traits.

My first experiment examined the relative importance of the contributions of duration and intensity to sediment disturbance effects on stream benthic biota. Artificial streams under controlled laboratory conditions were established to quantify the effects of sediment disturbances that differed in intensity and duration on different common benthic invertebrate taxa and periphyton. My results revealed that the relative effects of intensity and duration vary in relation to the response variable under consideration. This was the case even for those descriptors of the same biological component. For example, periphytic organic content and autotrophic index showed a strong positive rank correlation with increasing disturbance dose (*i.e.* the product of intensity and duration), while chlorophyll *a* content experienced a more complicated pattern driven by a greater relative effect of duration on this variable. This pattern of large deviations from dose-based expected scenarios was even more dramatic for invertebrate drift, for which some interactions between intensity and duration were found.

I then investigated under field conditions the mechanisms through which temporal variation in intensity within individual perturbations can mediate sediment disturbance effects on benthic invertebrate assemblages. Benthic assemblages in several flow-through channels were exposed to daily sediment pulses of equal intensity, duration and frequency but varying temporal pattern for five days. Recovery of benthic assemblages was subsequently followed for twelve days. Sediment pulses of variable intensity produced quantitatively (abundance) and qualitatively (structure and composition) stronger effects on invertebrate drift than pulses

of constant intensity. This was most likely a result of the resistance or avoidance capacity of invertebrates being surpassed by the greater maxima and higher variability of intensity under the temporally variable treatment. Further, I also found signs indicative of an effect of the temporal pattern within perturbations on post-disturbance recovery of invertebrate assemblages *in situ*.

I examined experimentally in the field the importance of temporal variability in the definition of the effect of combined sediment-nutrient disturbances on stream benthic assemblages. *In situ* artificial colonisation plots were exposed to regular and temporally variable sediment and nutrient regimes crossed in a fully-factorial experimental design for one month. Whereas temporal variability mediated the effect of sediment disturbances on most response variables, interactions between the temporal variability of sediment and nutrient regimes determined the effects of compounded disturbances on algal biomass and the diversity, taxonomic and trophic composition of benthic assemblages. These effects were driven by the combination of variable sediment and regular nutrient disturbance regimes, where an initial cluster of sediment perturbations seemed to create the necessary conditions for the subsequent effect of regular nutrient enrichment. These results suggest strongly that temporal variability can mediate the effects of multiple-stressor disturbances by altering the mode of action of their constituent stressors on ecosystems.

Overall, my research demonstrates that different temporal attributes of disturbances can mediate the effects of disturbances on local ecosystem processes. All temporal properties of disturbance tested experimentally demonstrated a capacity to mediate the nature and extent of responses of biotic assemblages through different but complementary mechanisms. Moreover, my results revealed the existence of novel causal mechanisms involving interactions of different temporal attributes with other disturbance traits and stressors. These results highlight the importance of incorporating the temporal dimension of disturbances into the study, prediction and management of ecological disturbances.

Acknowledgements

An incredible number of people have helped throughout the process of my PhD work. My sincere gratitude goes to you all. There are, however, a few people who deserve a special mention. I must first thank my wife Yukiko for her unconditional love, support and encouragement. You help me maintain perspective on life and remind me of what is really important. She also was a magnificent assistant in all the experiments that compose the work presented in this document. Nothing of this could possibly have been done without you my love. I am a lucky guy indeed.

I thank my supervisor Dr. Ian Donohue for guiding me with endless patience through all these years. His suggestions, continuous advice and encouragement to communicate my work through conferences and publications have made me a much better scientist and person. It has been an inspiration to work with a person of your enthusiasm and positivism. I also thank my committee members Dr. Ken Irvine and Professor Jim Wilson for their assistance and constructive comments offered through my PhD.

Peter Stafford deserves a paragraph to himself. This reflects the 24 hour logistical input and support he provided without which I could not have hoped to be as productive as I was. It is amazing how many things we could do with so little. Thanks Peter for all the alternative professions you have taught me. Should my career as scientist failed, I could always be a competent plumber, carpenter or gardener. But foremost, many thanks for being the wonderful person you are. You have been always source of support, much laughter and many good conversations over these years. I am still moved by that unexpected visit at Kippure in the middle of the night. Not many people would have made a two-hour night drive to bring us some pizza believing we had run out of food. My most sincere gratitude goes also to Mark Kavanagh and Alison Boyce. I really appreciate all your fresh ideas and altruistic help with my experiments guys.

Several other staff and student members in Zoology have contributed in one way or another to my work. It has been a great experience to be part of this department during all these years. I would like to give a very special thanks to all the wonderful people in the Freshwater Research Group. Girls, this dissertation would not have been possible without your support and friendship.

Meeting you all made worthwhile coming here. My close friends John O'Brien and Alberto Carreras Feiner deserve also separate acknowledgement. Thanks very much guys for your help inside and outside the academics and, most importantly, for your friendship and the many good moments shared.

Last but not least by any means, to my family. This work is based very much on your continuous trust and encouragement. I would like to express my sincere gratitude to my aunt Coro, for welcoming and making us feel at home during the last stage of my thesis writing. And of course to my mum and dad; you are the most supportive and loving parents anybody can possibly have. Thank you so much. This thesis is dedicated to you... and I promise to get a real job now.

This research was undertaken with the partial assistance provided by a Trinity College Postgraduate studentship held by the author.

Table of contents

Summary	iii
Acknowledgements	v
List of figures	ix
List of tables	xii
List of appendices	xiii
Chapter I. Introduction and thesis outline	1
Setting an ecological context: disturbance in the Anthropocene	3
Towards a standard characterisation of disturbance	7
Temporal attributes of disturbances: historical context and current status	11
Methodological approach	16
Research objectives and outline of this thesis	22
Chapter II. Differential contribution of intensity and duration to the ecological effects of disturbance	25
Abstract	27
Introduction	28
Methods	31
Experimental design	31
Statistical analysis	35
Results	36
Discussion	44
Chapter III. The temporal pattern of intensity within perturbation events regulates the effects of disturbances	51
Abstract	53
Introduction	55
Methods	59

Experimental design	59
Sampling and laboratory analysis	60
Statistical analysis	62
Results	64
Invertebrate drift	65
Benthic invertebrates <i>in situ</i>	70
Discussion	72
Chapter IV. Temporal variance mediates effects of compounded perturbations	78
Abstract	80
Introduction	81
Methods	83
Experimental design	83
Statistical analysis	87
Results	88
Discussion	96
Chapter V. General discussion	101
References	110
Appendices	149

List of figures

Chapter I

Figure 1.1. Simplified example of human alteration of natural disturbance regimes in a catchment managed for wood production 6

Figure 1.2. Conceptual cause-effect-response disturbance model 8

Figure 1.3. Schematic characterisation of a disturbance regime through its principal temporal properties (a) within and (b) among perturbation events 12

Figure 1.4. The mechanistic experimental approach used in this thesis to establish the effects of sediment disturbance temporal properties on stream benthic assemblages 22

Chapter II

Figure 2.1. (A) Design of the artificial stream sets (see *Experimental design* in Methods for explanation) and (B) example of distribution of suspended solid (SS) concentration and exposure time treatments (T) among experimental units 32

Figure 2.2. Mean (\pm SE) turbidity in artificial streams in each sediment concentration treatment 37

Figure 2.3. Mean (\pm SE) (A) periphyton chlorophyll *a*, (B) organic content, and (C) autotrophic index for each sediment concentration x exposure time treatment combination 38

Figure 2.4. Mean (\pm SE) number of drifting (A) *Baetis rhodani* (initial *n* = 5 per channel), (B) *Rhithrogena semicolorata* (*n* = 6), (C) *Aseillus aquaticus* (*n* = 10), and (D) *Glossosoma boltoni* (*n* = 10), and % of accumulated drift relative to initial *n* of (E) *B. rhodani*, (F) *R. semicolorata*, (G) *A. aquaticus*, and (H) *G. boltoni* as a function of suspended solid concentration and exposure time 42

Figure 2.5. Treatments ranked by sediment dose (concentration x exposure time) against mean (A) chlorophyll *a* concentrations and (B) % organic content of periphyton, (C) the autotrophic index, and (D) total invertebrate drift. Lines show rank relationship expected under the assumption of equality of effect between concentration and exposure time. 43

Chapter III

Figure 3.1. Schematic representation of (A) a disturbance regime with no temporal variability and (B) an equivalent regime in terms of disturbance duration, mean intensity and frequency with temporal variability occurring both within and among perturbations 57

Figure 3.2. (A) The distribution of sediment perturbations (black rectangles), drift samples (immediate: upper solid arrows, delayed: upper broken arrows) and benthic samples (lower dotted arrows), and (B) resulting mean (\pm SD, $n = 3$) daily turbidities in the constant (closed circle) and variable (closed square) disturbance treatments over the duration of the experiment 65

Figure 3.3. Mean (\pm SD) (A, B) rates and (C, D) rarefied taxon richness of invertebrates drifting from experimental channels during sediment addition (immediate drift; A, C) and during the time elapsed between consecutive pulses (delayed drift; B, D) 66

Figure 3.4. Mean (\pm SD) (A) abundance and (B) rarefied taxon richness of benthic invertebrates *in situ* immediately following cessation of sediment disturbances (Day 5) and during the subsequent recovery period (Day 10, Day 17) 71

Figure 3.5. Non-metric multidimensional scaling plots (calculated from Bray-Curtis similarity matrices based on $\log(x+1)$ -transformed abundance data) showing differences in the (A) composition and (B) trophic structure of invertebrate assemblages *in situ* after cessation of disturbances 72

Chapter IV

Figure 4.1. Schematic representation of experimental treatments resulting from a 3x3 full-factorial design crossing temporal patterns of sediment (filled squares) and nutrient (open squares) disturbance regimes with three levels each: regular (R), variable (V) and undisturbed (U) 84

Figure 4.2. Mean (\pm SD) (A) concentrations of periphytic chlorophyll *a* and (B) autotrophic index in each experimental disturbance regimes ($n = 4$) 89

Figure 4.3. Mean (\pm SD) (A) invertebrate abundance, (B) rarefied taxon richness and (C) Shannon’s diversity of benthic invertebrates in each experimental disturbance regime ($n = 4$) 92

Figure 4.4. Proportions of functional feeding groups in invertebrate assemblages in each experimental treatment 94

Figure 4.5. Mean (\pm SD) relative abundance of selected benthic invertebrate taxa in each experimental treatment ($n = 4$) 95

Chapter V

Figure 5.1. Generalised conceptual model representing the manner by which a disturbance regime composed of multiple agents of disturbance affects an ecosystem, causing a shift (ΔE) in its state driven by changes in its (A) abiotic and (B) biotic components 104

Figure 5.2. Schematic representation of direct (closed lines) and indirect (dashed lines) effects of sediment disturbance temporal properties on stream biota. Letters by the lines indicate the existence of interactive effects among corresponding properties 105

List of tables

Chapter I

Table 1.1. Principal attributes of disturbances and an associated non-exhaustive list of (a) theoretical (b) experimental and (c) observational ecological studies 9

Table 1.2. Effects of increased sediment loads on freshwater organisms (adapted from Donohue and García Molinos 2009) 18

Chapter II

Table 2.1. Results of ANOVA for effects of suspended solid concentration and exposure time on periphyton and macroinvertebrate drift 39

Chapter III

Table 3.1. Results of ANOVA examining the effects of sediment disturbance pattern on the abundance and rarefied taxon richness of invertebrate drift and benthic assemblages *in situ* 67

Table 3.2. Results of PERMANOVA examining the effects of sediment disturbance pattern on the assemblage composition and trophic structure of invertebrate drift and benthic assemblages *in situ* 68

Table 3.3. Principal (≥3%) invertebrate taxa contributing (SIMPER) to observed significant differences in assemblage composition of immediate drift and their percentage contribution to the pairwise difference between treatments 69

Chapter IV

Table 4.1. Results of ANOVA examining the effects of experimental treatments on periphyton and benthic invertebrates 90

Table 4.2. Results of SNK *post hoc* tests elucidating the interactions between sediment and nutrient disturbance regimes on (A) periphyton chlorophyll *a*, (B) benthic invertebrate diversity (Shannon’s index) and the (C) taxonomic and (D) trophic composition of benthic invertebrate assemblages 91

Table 4.3. Results of PERMANOVA examining the effects of experimental treatment on the taxonomic and trophic composition of benthic invertebrate assemblages 94

List of appendices

Appendix A. List of macroinvertebrate taxa and respective functional feeding groups (FFG) identified in drift and benthic samples during the experiment presented in Chapter III 150

Appendix B. List of macroinvertebrate taxa and corresponding functional feeding groups found in benthic samples during the experiment presented in Chapter IV 152

Chapter I. Introduction and thesis outline



Stream bank collapsed as a result of unrestricted access to the stream by cattle
(Photo by Jorge García Molinos)

This thesis explores the importance of temporal properties of disturbances for regulating the responses of ecosystems to perturbations. This is a particularly important issue in ecology given the accelerating alteration of disturbance regimes by global human environmental change. I followed a mechanistic experimental approach to examine, through successive laboratory and field experiments, the contribution of different temporal properties to sediment disturbance effects on stream benthic assemblages. Importantly, my experimental designs allowed me to unconfound temporal cause and effect relationships from those of other disturbance traits.

Setting an ecological context: disturbance in the Anthropocene

A few years ago, Crutzen (2002) introduced the term Anthropocene to describe the current geological epoch and to emphasise the growing human domination of the global environment, which is arguably the most pressing problem facing humanity (Hannah *et al.* 1994, Vitousek *et al.* 1997, Sanderson *et al.* 2002, Steffen *et al.* 2007). The consequences of human-derived global environmental change therefore, while still little understood, are of the greatest importance for biodiversity (Chapin *et al.* 2000, Sala *et al.* 2000, Thomas *et al.* 2004), ecosystem functioning (Chapin *et al.* 1997) and, ultimately, human welfare (Costanza and D'Arge 1997, Chivian 2001, Erb *et al.* 2009). Understanding the nature and extent of human-induced environmental change comprises an urgent need for ecologists and environmental managers alike (Lubchenco 1998, Sala *et al.* 2000). Key to this is the ability to identify and define the mechanisms by which disturbances affect fundamental ecosystem processes (Bengtsson *et al.* 2000, Brawn *et al.* 2001, Zhibin *et al.* 2006).

Natural communities are highly dynamic both in space and time (Southwood 1996). One of the primary goals of community ecology is that of understanding patterns of biotic diversity, composition and stability in nature and identifying the processes that sustain and modify those patterns. Current theory considers community dynamics as the product of species responses to a combination of simultaneously operating stochastic (unpredictable) and deterministic (predictable) factors (Hubbell 2001, Chave *et al.* 2002, Chase 2007, Ellwood *et al.* 2009, Mutshinda *et al.* 2009). Stochastic factors comprise the processes of birth, mortality, dispersal, extinction and speciation; which operate similarly across all species (Bell 2001, Hubbell 2001, Chave 2004). In contrast,

deterministic factors include differential patterns of niche structure and density-dependent interactions (Chesson 1986, Chesson 1994, Chesson 2000, Chase and Leibold 2003, Condit *et al.* 2006, McGill *et al.* 2006). In this context, disturbance or stress (*sensu* Underwood 1989) can be seen as an extreme of the natural heterogeneity continuum from both deterministic (Karr and Freemark 1985, Underwood 1989) and stochastic (Lande *et al.* 2003) perspectives. Disturbances therefore comprise important drivers of evolution (Suchanek 1981, Levin 2004) and biological structure for populations (Lodge and Kelly 1985, Piazzini *et al.* 2004, Pathikonda *et al.* 2009), communities (McAuliffe 1984b, Goldberg and Gross 1988, Airoldi 1998, Collins 2000) and ecosystems (Connell 1978, Bengtsson *et al.* 2000, Botta and Foley 2002).

The effects of natural disturbances on biotic communities have largely directed the development of theory in disturbance ecology (*e.g.* Dayton 1971, Holling 1973, Connell 1978, Huston 1979, Platt and Connell 2003, Roxburgh *et al.* 2004). Research into the effects of human disturbances has generally followed a parallel, often unconnected, path under other ecological disciplines, primarily conservation ecology (*e.g.* Hansen *et al.* 1991, Salomons 1995, Barton and Farmer 1997, Groffman *et al.* 2006) and ecotoxicology (*e.g.* Murray-Gulde *et al.* 2002, Hoang *et al.* 2007). This dichotomy is likely attributable to the general conceptualisation of human disturbances as purely destructive forces in contrast to the broader ecological role given to natural disturbances (Pickett and White 1985). However, although the mode of action and the characteristics of anthropogenic perturbations may differ from those of natural disturbances (Walker and Willing 1999, Lindenmayer and McCarthy 2002, Elliot 2006), both types of disturbance are strongly related (Fig. 1.1); increasing human alteration of the environment continuously modifies the magnitude, extent and temporal pattern of natural disturbance regimes both at local

(Swanson and Dyrness 1975, Yin and Li 2001, Allan 2004, Mailhot *et al.* 2007, Syphard *et al.* 2007) and global (Michener *et al.* 1997, Christensen and Christensen 2003, Lowe and Gregory 2005) scales. Setting boundaries between natural and human disturbances under such circumstances is, therefore, very difficult (Walker and Willing 1999, White and Jentsch 2001). Thus, these peculiarities make crucial the incorporation of anthropogenic factors into the study of the ecology of disturbances (*e.g.* Chapin *et al.* 1993, Benedetti-Cecchi *et al.* 2006, Enberg *et al.* 2006, Saltz *et al.* 2006). As White and Bratton (1980) noted insightfully, the preservation of natural systems necessarily involves the paradox of seeking to preserve systems that change. Therefore, efforts should be directed primarily towards predicting and mitigating those changes that are not natural to the system (Underwood 1989).

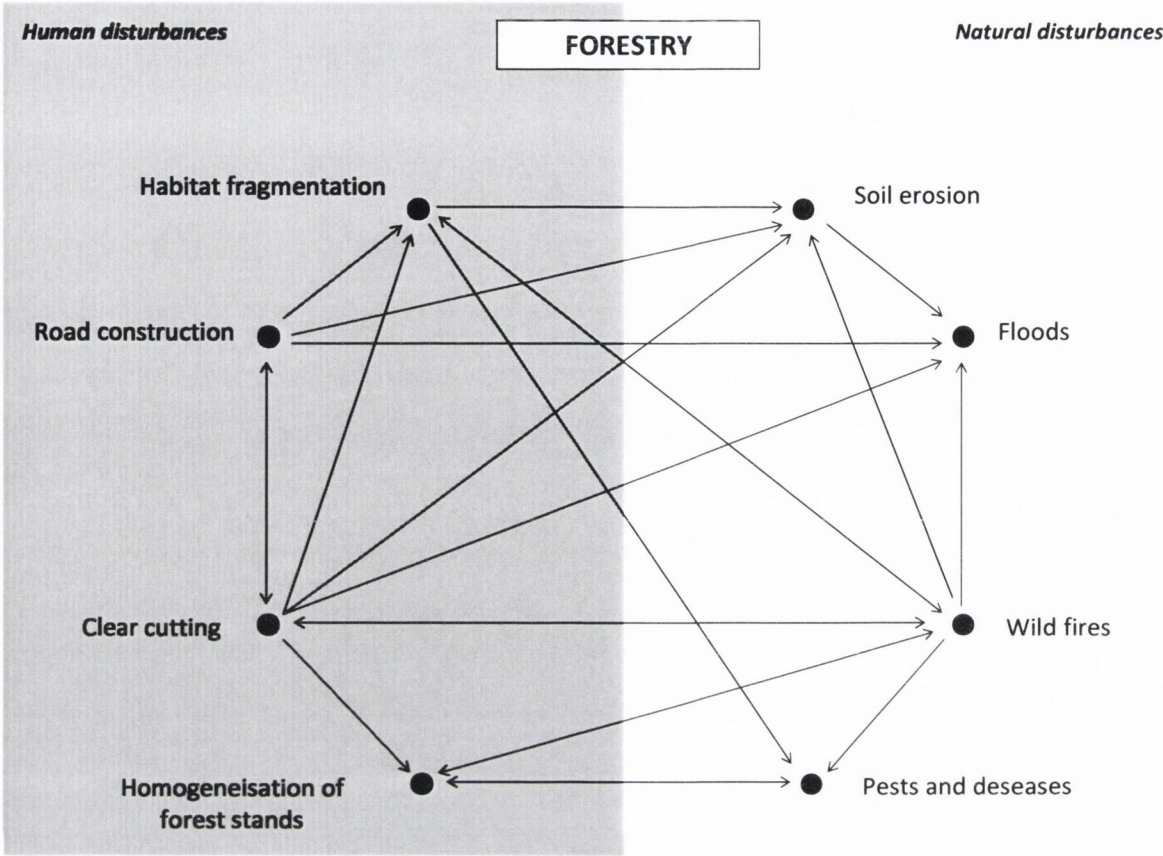


Fig 1.1. Simplified example of human alteration of natural disturbance regimes in a catchment managed for wood production. The alteration of ecosystem processes by anthropogenic activities results from both direct environmental impacts (human disturbances) and indirect modifications of the composition, magnitude, temporal and spatial patterns of natural perturbations. For example, activities such as clear-cutting or road-building denude the landscape of vegetation and perturb the hydrologic cycle within the catchment. The interception losses of precipitation are reduced and a greater proportion of rainfall reaches the soil mantle. The infiltration capacity of compacted and structurally altered soils is then rapidly surpassed and a greater proportion of the precipitation flows overland. As a result, natural events such as surface erosion, mass soil movements and stream floods are altered with a tendency towards more frequent and intense events.

Towards a standard characterisation of disturbance

What is considered a disturbance has been matter of much debate (*e.g.* Sousa 1984, Rykiel 1985, van der Maarel 1993, White *et al.* 1999, White and Jentsch 2001). A commonly cited definition is that of Pickett and White (1985), which presents disturbance as 'any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment'. As opposed to the perception of disturbance as a phenomenon causing departure from the normal set of conditions of an ecosystem (*e.g.* Odum *et al.* 1979), the importance of this definition lies in stressing disturbance as an event causing measurable physical changes in the structure of biotic assemblages and environmental variables. Criticism of this general definition is centred on the fact that, if disturbances are to be defined merely by their biological effects (*e.g.* Bender *et al.* 1984, Speidel 2001, Suding and Goldberg 2001), we cannot directly relate the consequent changes to the process(es) responsible for their generation and maintenance (van der Maarel 1993, Lake 2000). This inability to establish cause to effect (and response) relationships inhibits the capacity to develop generality in disturbance ecology (White and Jentsch 2001, Johnson and Miyanishi 2007). The study of ecological disturbances requires, therefore, consideration of each of the components involved in the disturbance process; the disturbance itself, the disruption produced on the ecological system and the subsequent consequences of this disruption (cause-effect-response model; Fig. 1.2). The development of knowledge in disturbance ecology requires, therefore, the analysis of disturbance effects in relation to their different constituent properties (White and Jentsch 2001), which can themselves be grouped into three major dimensions (Table 1.1); magnitude, time and space. Though research in this direction has been prolific in

Table 1.1. Principal attributes of disturbances and an associated non-exhaustive list of (a) theoretical (b) experimental and (c) observational ecological studies.

Attribute	Dimension	Definition	References
Intensity	Magnitude	Strength of a perturbation	<p>(a) Connell 1978, Malanson 1984, Quintana 2002, Yoshida 2006</p> <p>(b) Sommer 1995, McCabe and Gotelli 2000, Collins <i>et al.</i> 2001, Dahlberg <i>et al.</i> 2001, Elliott <i>et al.</i> 2001, Hickman and Hartnett 2002, Kennard <i>et al.</i> 2002, Lenz <i>et al.</i> 2004a, Wernberg and Connell 2008</p> <p>(c) Townsend <i>et al.</i> 1997, Norkko <i>et al.</i> 2006</p>
Extent	Space	Area affected by a perturbation	<p>(a) Miller 1982, Kirk and Levin 1996, Bascompte and Solé 1998, Flather and Bevers 2002, Alados <i>et al.</i> 2009</p> <p>(b) Shure and Phillips 1987, Smith and Brumsickle 1989, Whitlatch <i>et al.</i> 1997, McCabe and Gotelli 2000, Cristoni <i>et al.</i> 2004, Wernberg and Connell 2008, Svensson <i>et al.</i> 2009</p> <p>(c) Hiura 1995</p>
Spatial pattern	Space*Magnitude	Spatial variation in intensity of a disturbance event	<p>(a) Benedetti-Cecchi 2000, Adler <i>et al.</i> 2001, Benedetti-Cecchi 2003</p> <p>(b) Sommer 2000, Benedetti-Cecchi <i>et al.</i> 2005</p>
Frequency	Time*Magnitude	Number of events per unit time	<p>(a) Connell 1978, Huston 1979, Clark 1996, Kirk and Levin 1996, Sohngen and Haynes 1997, Kondoh 2001, Wei <i>et al.</i> 2003</p> <p>(b) Collins 1992, Sommer 1995, Navarrete 1996, Collins 2000, McCabe and Gotelli 2000, Collins <i>et al.</i> 2001, Elliott <i>et al.</i> 2001, Lenz <i>et al.</i> 2004b, Collins and Smith 2006, Heather <i>et al.</i> 2008, Svensson <i>et al.</i> 2009</p> <p>(c) Meffe 1984, Townsend <i>et al.</i> 1997</p>

Table 1.1. Continued.

Temporal variability or predictability	Time	Variance in the mean time between perturbations	(a) Poff and Ward 1989, Caswell and Cohen 1995, Benedetti-Cecchi 2003 (b) Robinson and Sandgren 1983, Bertocci <i>et al.</i> 2005, Benedetti-Cecchi <i>et al.</i> 2006, Diamond <i>et al.</i> 2006, Atalah <i>et al.</i> 2007, Bertocci <i>et al.</i> 2007, Cifuentes <i>et al.</i> 2007, Sugden <i>et al.</i> 2007, Wollgast <i>et al.</i> 2008
Timing or temporal sequence	Time	Moment of occurrence of perturbations relative to species physiological or biological needs	(a) Iwasa and Levin 1995 (b) Airoidi 2000, Crawley 2004, Atalah <i>et al.</i> 2007, Cifuentes <i>et al.</i> 2007, Sugden <i>et al.</i> 2007, Wollgast <i>et al.</i> 2008
Duration	Time	Temporal length of a perturbation	(a) Bender <i>et al.</i> 1984, Poff and Ward 1989, Newcombe and McDonald 1991, Newcombe and Jensen 1996, Bell <i>et al.</i> 2003, Newcombe 2003 (b) Shaw and Richardson 2001, Notestein <i>et al.</i> 2003, Hewitt and Norkko 2007
Temporal pattern	Time*Magnitude	Temporal variation in intensity of a disturbance event	(a) Lake 2000 (b) Imbert and Perry 2000, Klironomos <i>et al.</i> 2005 (c) Hewitt and Norkko 2007, Crosa <i>et al.</i> 2010

Temporal attributes of disturbances: historical context and current status

Disturbance-induced temporal variability in resources, environmental conditions and biological processes comprises one of the principal mechanisms structuring ecological systems (Chase and Leibold 2003, Roxburgh *et al.* 2004, Shea *et al.* 2004). Hence, ecosystem structure and functioning are often reliant on the specific periodicity, timing and duration of natural disturbance regimes (*e.g.* Hughes and Rood 2003, Pausas *et al.* 2004). Global alterations of disturbance regimes under future land-use and climate change scenarios frequently, however, predict increased temporal variability, with striking consequences (*e.g.* Webster *et al.* 2005, Saltz *et al.* 2006, Syphard *et al.* 2009). Robust understanding and prediction of the effects of temporally variable disturbances is, therefore, essential for effective environmental management and conservation.

The temporal dimension of a disturbance regime can be viewed conceptually as a combination of the properties that describe its temporal context both within and among individual perturbations (Fig. 1.3). Among them, frequency has monopolised the interest of ecologists from an early stage. This is probably a consequence of its key role in central ecological theories developed during the 1970s (*e.g.* Connell 1978, Huston 1979), which predict maximum diversity at intermediate levels of disturbance (*i.e.* diversity is reduced at high frequencies by reduction or extinction of populations and at low frequencies by competitive exclusion). Under this theoretical framework, a large body of literature has evolved demonstrating the prominent role of disturbance frequency on multiple ecological processes such as patch dynamics (Roxburgh *et al.* 2004), life history strategies (Meffe 1984), community succession (Collins and Smith 2006), and ecosystem energetics (Sohngen and Haynes 1997).

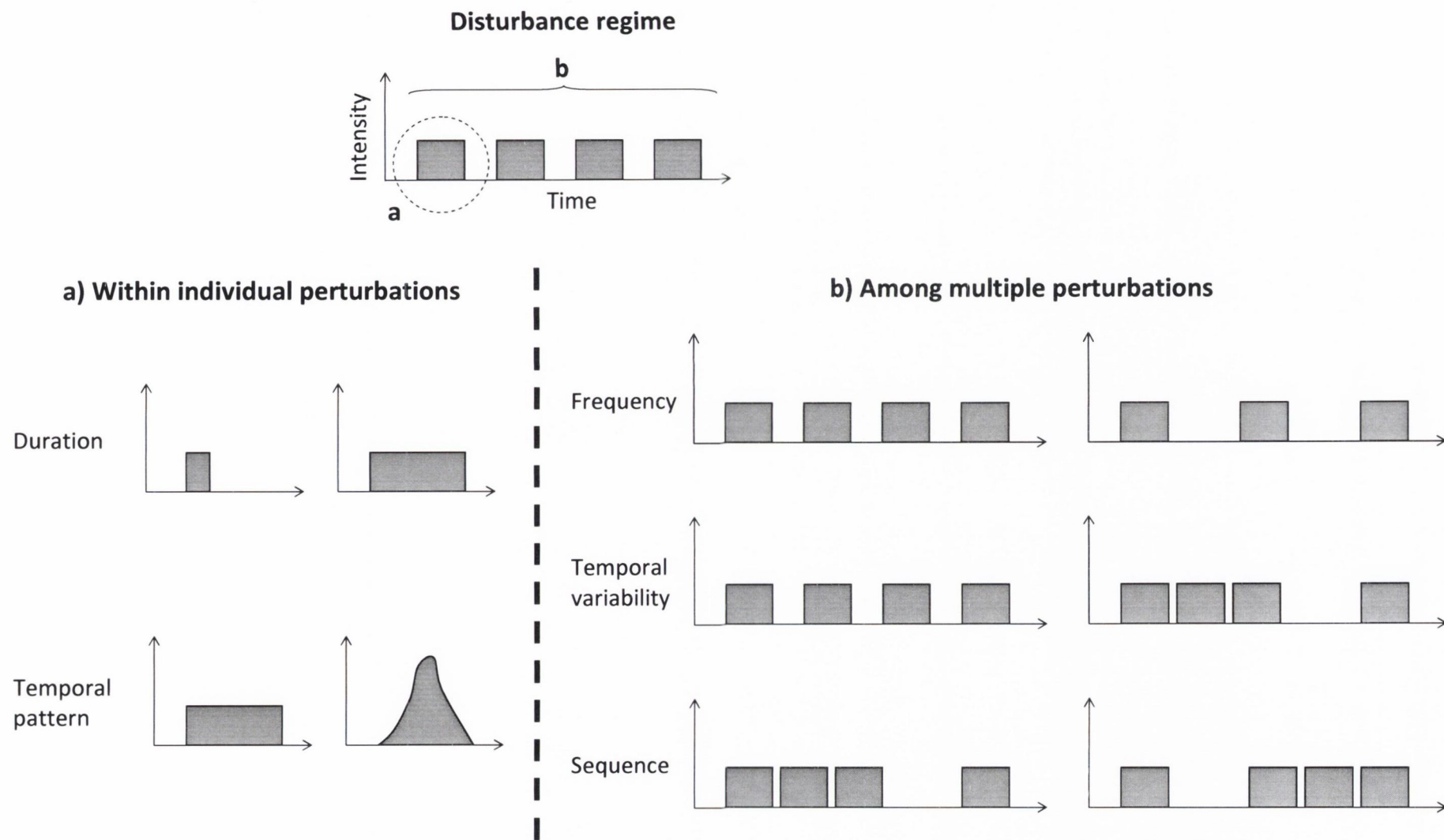


Fig. 1.3. Schematic characterisation of a disturbance regime through its principal temporal properties (a) within and (b) among perturbation events.

Since the 1980s, an emerging awareness of the importance of the variability of ecological patterns and processes in ecology (*e.g.* Chesson 1985, Chesson 1986, McArdle *et al.* 1990, Gaston and McArdle 1993, Horne and Schneider 1995, Palmer *et al.* 1997, Micheli *et al.* 1999) produced a growing interest in the study of the spatiotemporal variability associated with disturbance regimes (*e.g.* Robinson and Sandgren 1983, Butler 1989, Navarrete 1996). The use of frequency as a descriptor of temporal variability is, however, limited by the fact that it confounds the temporal and magnitude dimensions of a regime (*i.e.* increasing frequency increases both the number of events per unit of time and the overall intensity of the process). As a result, Benedetti-Cecchi (2000, 2003) proposed considering the variance of frequency as an alternative descriptor of the temporal variability associated with disturbance regimes. High temporal variance implies the clustering of several perturbations over short periods of time alternating with long undisturbed periods (Fig. 1.3). Subsequent studies (Bertocci *et al.* 2005, Benedetti-Cecchi *et al.* 2006, Bertocci *et al.* 2007) have shown that changes in the temporal variance of disturbance regimes mediate changes in the structure and composition of biotic assemblages independently of the intensity of the regime (but see Atalah *et al.* 2007, Cifuentes *et al.* 2007, Sugden *et al.* 2007, Wollgast *et al.* 2008). These changes may be influenced, however, by how the timing of occurrence of individual perturbations matches or mismatches periods of growth, reproduction and recruitment of organisms. In this case, it may be the specific sequence of disturbances (Fig. 1.3) rather than temporal variation that affects the stability of ecological systems (Dayton *et al.* 1984, Iwasa and Levin 1995, Airolidi 2000, Crawley 2004, Atalah *et al.* 2007, Cifuentes *et al.* 2007). Moreover, the specific timing of perturbations may also be very important in determining the combined effect of compounded disturbance (or multiple stressor) regimes. Resulting ecological patterns can follow different trajectories depending on the

order with which each stressor acts and the extent to which their relative effects are conditioned by preceding disturbance events (Paine *et al.* 1998, Hughes and Connell 1999, Fukami 2001).

Little empirical work has been done which examines the effects of properties that define the temporal context of individual disturbance events (Table 1.1), namely their duration and temporal pattern (Fig. 1.3). Shaw and Richardson (2001) demonstrated how the duration of sediment disturbances of constant intensity regulated the effects of disturbance on freshwater benthic invertebrate assemblages and trout growth. Hewitt and Norkko (2007) found that increased duration of exposure to sediment disturbance altered the feeding habits of two marine bivalves by decreasing their filtration rates. Whereas these results suggest an effect of duration on biological responses independent of the intensity of disturbances, the interplay between duration and intensity remains to be tested in disturbance ecology. Different toxicological studies demonstrate that the relative contribution of duration and concentration to toxicity is frequently highly variable in relation to the different modes of action of each toxicant (*e.g.* Weller *et al.* 1999, Coman *et al.* 2005, Hoang *et al.* 2007). Toxicants with low acute to chronic ratios are thought to have modes of action that allow them to reach target sites faster, therefore involving higher toxicity effects of concentration compared to duration (Diamond and Butcher 2003). By extension, it appears likely that the relative contribution of duration and intensity to disturbance effects depends on the specificity and mode of action of the disturbance relative to the disturbed system.

Concentrations of common air and water pollutants in the environment are rarely constant but usually exhibit high variability depending upon their incorporation rates

from point and diffuse sources (*e.g.* Krause 1995, Haygarth and Jarvis 1997, Donohue *et al.* 2005, Banas *et al.* 2008, Kayhanian *et al.* 2008). Examples of disturbance events characterised by temporally variable patterns of intensity are also common to natural disturbances. The intensity of large-scale fires, for example, varies over time as a result of variation in fuel loads and weather conditions (Johnson 1992, Schwilk 2003). Little is known, however, about the effect on ecological patterns of varying the temporal pattern of intensity within individual perturbations. Hewitt and Norkko (2007) documented different patterns in the biomass accrual of two species of marine bivalve as a result of temporal fluctuations in ambient suspended sediment concentrations. Further, Crosa *et al.* (2010) attributed reductions in fish and invertebrate abundance downstream of an alpine reservoir to sharp peaks in suspended solid concentrations of short duration from free-flow flushing operations. Similarly, Imbert and Perry (2000) found that abrupt changes in non-scouring flow produced a strong increase in the abundance of invertebrate drift. Interestingly, the peak in drift resulting from gradual flow increments was not only comparatively smaller, but it also occurred much later. The heterogeneity associated with the temporal patterning of disturbance events also appears to have important effects at the global scale. Klironomos *et al.* (2005) demonstrated with an elegant experiment the important bias that can be introduced in long-term climate change predictions depending on the temporal patterning of the disturbance generated. They found significantly different structural and functional responses of a fungal community exposed to either a single-step increase in CO₂ concentrations or to gradual increases over a period of 6 years (equivalent to 21 generations).

In summary, with the arguable exception of frequency, current knowledge of the mechanisms by which temporal attributes of disturbance operate is still scarce and

mostly unconnected. Identifying and understanding the different mechanisms that generate and maintain disturbance-related ecological patterns is, however, a necessary first step towards a more holistic and precise assessment of the effects of disturbance on fundamental ecosystem processes (White and Jentsch 2001). Experimental studies designed to elucidate the relative importance of temporal properties of disturbances are, therefore, necessary to address important gaps in knowledge and to generate new research directions.

Methodological approach

Owing to the importance of water as a primary resource for humans, freshwater bodies are amongst the most endangered ecosystems in the world (Postel *et al.* 1996, Ricciardi and Rasmussen 1999, Dudgeon *et al.* 2006). Of the many anthropogenic stressors impacting freshwater ecosystems, increased sediment loading comprises one of the most widespread and pervasive forms (Waters 1995, Donohue and García Molinos 2009). Alterations of sediment delivery patterns often result from changes in land use practices, where the original catchment morphology and vegetal cover have somehow been modified by forms more susceptible to erosion (*e.g.* Quinn and Stroud 2002, Sutherland *et al.* 2002, Dearing and Jones 2003, Donohue *et al.* 2003a). The causes and deleterious effects of fine sediment suspension and deposition on the ecology of aquatic ecosystems have been widely reported (Table 1.2) and periodically reviewed (Chutter 1969, Alabaster 1972, Bruton 1985, Ryan 1991, Wood and Armitage 1997, Lind 2003, Donohue and García Molinos 2009). Because of the scale, ubiquity, pervasiveness and non-specificity of its mode of action, increased sediment loading comprises, therefore, an ideal agent of disturbance for experimentation.

Benthic invertebrates are, together with fish, the organisms used most frequently to assess the biological impacts of increased sediment loading on freshwater ecosystems (Table 1.2). Benthic invertebrates also present, unlike fish, major advantages for the purposes of disturbance experimentation because of their abundance, diversity, ease of collection, limited mobility, cosmopolitan distribution and relatively well-defined taxonomy, biology and ecology (Rosenberg and Resh 1993). In this thesis, I used a mechanistic experimental approach (Schoener 1986, Root and Schneider 1995) to examine the importance of temporal patterns of sediment disturbances on aquatic biota, focusing particularly on benthic invertebrate assemblages. This comprises a reductionist approach based on the identification of a set of critical causal relationships that are potentially responsible for the particular process of interest on which specific hypotheses are developed and tested through successive experiments, each with different but complementary interconnected goals. Implicit in this task is the capacity to unconfound cause-effect relationships between the experimental predictor and response variables from other environmental variables. Model laboratory systems and field mesocosms comprise appropriate tools for this purpose because they offer the highest degree of manipulative and control capacity along the continuum of experimental approaches yet they can retain sufficient realism to allow comparison and extrapolation to larger scales (Odum 1984, Lawton 1995).

Table 1.2. Effects of increased sediment loads on freshwater organisms (adapted from Donohue and García Molinos 2009).

Description	References
<i>I. Primary producers</i>	
Changes in photosynthetic activity	Meyer and Heritage 1941, Van Nieuwenhuysse and LaPerriere 1986, Davies-Colley <i>et al.</i> 1992, Izaguirre <i>et al.</i> 2009
Reduction in biomass	Van Nieuwenhuysse and LaPerriere 1986, Cuker 1987, Cuker <i>et al.</i> 1990, Horner <i>et al.</i> 1990, Davies-Colley <i>et al.</i> 1992, Yamada and Nakamura 2002, Francoeur and Biggs 2006, Izaguirre <i>et al.</i> 2009
Reduction in organic content	Cline <i>et al.</i> 1982, Graham 1990, Davies-Colley <i>et al.</i> 1992, Vuori and Joensuu 1996, McIntyre <i>et al.</i> 2005
Reduction in primary production	Van Nieuwenhuysse and LaPerriere 1986, Cuker 1987, Cuker <i>et al.</i> 1990, Finger <i>et al.</i> 2007
Morphological alterations of individual taxa	Wilson <i>et al.</i> 1999
Changes in abundance, diversity and/or community structure	Hansmann and Phinney 1973, Cline <i>et al.</i> 1982, Cuker <i>et al.</i> 1990, Burkholder and Cuker 1991, Cuker and Hudson 1992, Wulff <i>et al.</i> 1997, Izaguirre <i>et al.</i> 2009, Licursi and Gómez 2009
<i>II. Benthic invertebrates</i>	
Reduced feeding rates	Grazers: Broekhuizen <i>et al.</i> 2001, Donohue and Irvine 2004b, Peeters <i>et al.</i> 2006 Filter feeders: Loosanoff and Tommers 1948
Increased mortality	Ellis 1936, Broekhuizen <i>et al.</i> 2001, Gilmour 2002, Donohue and Irvine 2003, 2004b
Lower metabolic rates	Aldridge <i>et al.</i> 1987
Reduced viability of eggs	Harrison and Farina 1965
Decreased growth rates	Höss <i>et al.</i> 1999, Broekhuizen <i>et al.</i> 2001, Peeters <i>et al.</i> 2006
Enhanced waste production by filter feeders	MacIsaac and Rocha 1995

Table 1.2. Continued.

Description	References
Increased incidence of infection and infestation	Lemly 1982, McIntyre <i>et al.</i> 2005
Clogging of interstices and interference with oxygen availability	Chutter 1969, Lemly 1982, Radwell and Brown 2006, Bo <i>et al.</i> 2007
Decreased connectivity among appropriate habitat patches	Cohen 1995
Alterations to habitat structure and reduced habitat heterogeneity	Chutter 1969, Boles 1981, Erman and Erman 1984
Enhanced invertebrate drift	Ciborowski <i>et al.</i> 1977, Rosenberg and Wiens 1978, Culp <i>et al.</i> 1986, Shaw and Richardson 2001, Suren and Jowett 2001, Gibbins <i>et al.</i> 2007a
Colonisation patterns	Suren 2005
Changes in abundance, diversity and/or community structure	Cline <i>et al.</i> 1982, Lemly 1982, Culp <i>et al.</i> 1986, Quinn <i>et al.</i> 1992, Richards <i>et al.</i> 1993, Donohue <i>et al.</i> 2003b, Donohue and Irvine 2004a, Downes 2006, Matthaei <i>et al.</i> 2006, Connolly and Pearson 2007, Crosa <i>et al.</i> 2010
<i>III. Fish</i>	
Reduced survival of eggs and larvae	Turnpenny and Williams 1980, Cambray 1983, Wilber 1983, Reynolds <i>et al.</i> 1989, Servizi and Martens 1991, 1992, Galbraith <i>et al.</i> 2006
Gill damage and increased gill-flaring	Herbert and Merkens 1961, Berg and Northcote 1985, Reynolds <i>et al.</i> 1989, Martens and Servizi 1993, Sutherland and Meyer 2007

Table 1.2. Continued.

Description	References
Reduced individual growth rates, decreased maximum size and reduced length at sexual maturity	Herbert and Richards 1963, Sykora <i>et al.</i> 1972, Crouse <i>et al.</i> 1981, Gardner 1981, Wilber 1983, Sigler <i>et al.</i> 1984, Bruton 1985, McLeay <i>et al.</i> 1987, Miner and Stein 1993, Shaw and Richardson 2001, Suttle <i>et al.</i> 2004, Sutherland and Meyer 2007
Increased mortality	Wallen 1951, Herbert and Merkens 1961, Herbert and Richards 1963, Bruton 1985, McLeay <i>et al.</i> 1987, Suttle <i>et al.</i> 2004, Crosa <i>et al.</i> 2010
Emigration from affected areas	Sigler <i>et al.</i> 1984
Impaired feeding activity	Vinyard and O'Brien 1976, Confer <i>et al.</i> 1978, Berg and Northcote 1985, McLeay <i>et al.</i> 1987, Crowl 1989, Gregory and Northcote 1993, Gregg <i>et al.</i> 1997, Utne 1997, Rowe and Dean 1998, Sweka and Hartman 2001, De Robertis <i>et al.</i> 2003, Shoup and Wahl 2009
Induced colour changes	Herbert and Merkens 1961, McLeay <i>et al.</i> 1987
Instigation of stress responses such as increased blood sugar levels	McLeay <i>et al.</i> 1987, Servizi and Martens 1992
Increased susceptibility to toxicants	McLeay <i>et al.</i> 1987
Disrupted migration patterns through avoidance	Bruton 1985, Boubée <i>et al.</i> 1997, Richardson <i>et al.</i> 2001
Altered territorial behaviour	Berg and Northcote 1985
Altered breeding behaviour	Wilber 1983

Table 1.2. Continued.

Description	References
Increased incidence of infection	Herbert and Merkens 1961, Alabaster 1972, Servizi 1991
Increased risk of injury through increases in aggressive interactions among fish	Suttle <i>et al.</i> 2004
Altered predator avoidance behaviour	Gregory 1993, Lehtiniemi <i>et al.</i> 2005
Changes in abundance, diversity and/or community structure	Berkman and Rabeni 1987, Rabeni and Smale 1995, Rodríguez and Lewis 1997, Donohue <i>et al.</i> 2003b, Walters <i>et al.</i> 2003, Mol and Ouboter 2004, Crosa <i>et al.</i> 2010

Research objectives and outline of this thesis

This thesis aims to elucidate the importance of different temporal properties of disturbances by examining the effects of sediment disturbances on stream benthic assemblages. Although this research was conducted at particular spatial and temporal scales and focused primarily on a single agent of disturbance, it addresses the more general problem of whether the management of ecological disturbances should take into consideration their temporal dimension. The structure of this thesis conforms to an experimental mechanistic approach where all research hypotheses and, by extension, all experiments designed to test them, were framed in relation to the main objective (Fig. 1.4).

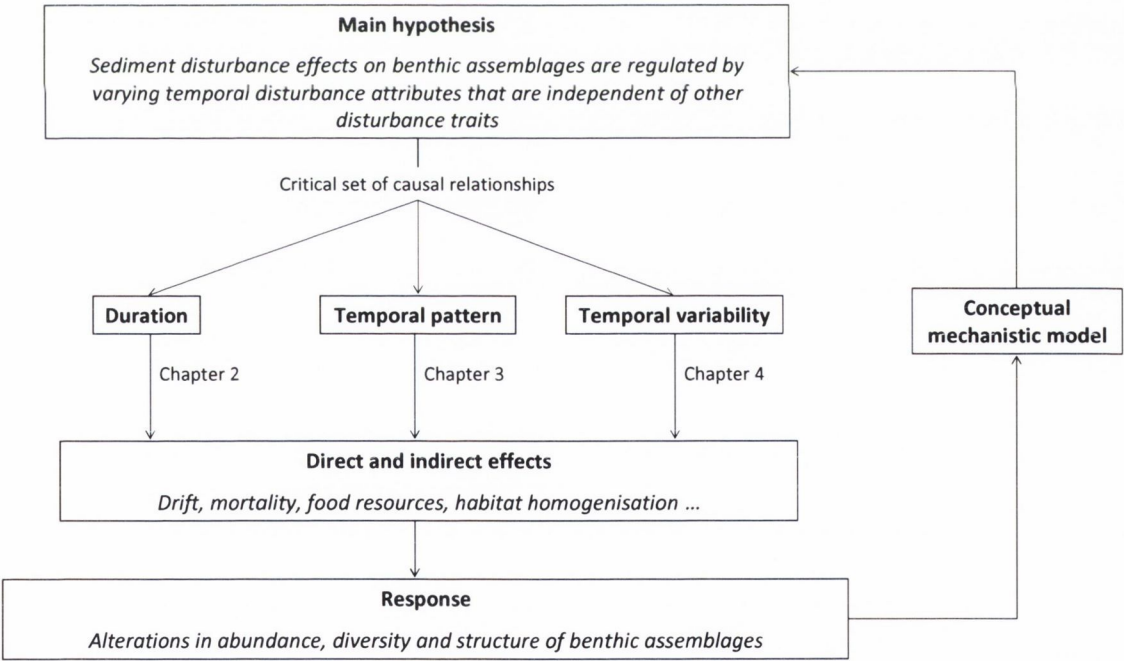


Fig. 1.4. The mechanistic experimental approach used in this thesis to establish the effects of sediment disturbance temporal properties on stream benthic assemblages.

My research hypotheses were tested as follows:

Hypothesis 1: *The ecological effects of disturbance depend on the specific combination of the intensity and duration of perturbations.*

Despite its theoretical interest, the relationship between disturbance duration and intensity has never been addressed explicitly in disturbance ecology. The effects exerted by a disturbance may be different in relation to the specific combination of duration and intensity depending on its mode of action and the susceptibility of the disturbed system. In Chapter 2, I describe how I used artificial stream channels to study, under controlled laboratory conditions, the relative and combined contribution of intensity and duration to sediment disturbance effects on stream benthic biota.

Hypothesis 2: *The temporal pattern of intensity within perturbations drives ecosystem responses to disturbance.*

Because the strength of a disturbance can vary over its duration (*e.g.* Zhang *et al.* 1997, Potter *et al.* 2006, Musolff *et al.* 2009), the temporal distribution of intensity within a perturbation may influence the nature and extent of its effects. I examine this in Chapter 3, where I describe the results of a field experiment using in-stream flow-through channels used to test the effects of two sediment disturbances of contrasting temporal pattern on benthic assemblages.

Hypothesis 3: *The effects of multiple stressors on ecosystems depend upon the interaction between their respective temporal patterns.*

High temporal variability clusters successive perturbations in time and influences system recovery by regulating the time interval between consecutive perturbations (Benedetti-Cecchi 2003). One of the principal features that characterises human disturbances is that they are often composed of a combination of multiple stressors (Crain *et al.* 2008, Klok and Kraak 2008). Under a scenario where multiple agents of disturbance are acting concurrently at a particular spatial and temporal scale, temporal heterogeneity in the occurrence of perturbations could comprise a key driver of the resulting combined effects. I test this in Chapter 4 using a field experiment in which benthic stream assemblages in colonisation cages were exposed to sediment and nutrient perturbations, either in isolation or compounded, of different stochasticity (regular versus variable temporal regimes).

The findings of Chapters 2, 3 and 4 are brought together in Chapter 5 where their implications for the main research hypothesis of this thesis and their potential applications to management are discussed.

Chapter II. Differential contribution of intensity and duration to the ecological effects of disturbance



Artificial stream channels used in the experiment with details of channels under the lowest (+0 mg L⁻¹ sediment) and highest (+2000 mg L⁻¹) intensity treatments
(Photo by Jorge García Molinos)

Although theory predicts that the duration of perturbations is an important determinant of their effects, little empirical work has tested this assertion. Further, the possibility of interactive effects between the intensity of perturbations and their duration remain untested at the level of the ecological community. In this chapter, I describe how I examined whether the responses of benthic biota to sediment disturbances are driven by the specific combination of intensity and duration.

Abstract

An importance of the duration associated with a perturbation in the definition of ecological responses to natural and anthropogenic disturbances has been indicated by theory. However, it has received little experimental examination. Further, the relationship between the duration and intensity of a disturbance is of special interest because it defines the dose acting upon the receiving system. I conducted an experiment in artificial streams under controlled laboratory conditions to quantify the response of four common macroinvertebrate taxa (*Rhithrogena semicolorata*, *Baetis rhodani*, *Asellus aquaticus*, and *Glossosoma boltoni*) and benthic algae to doses of inorganic sediment that differed in maximum concentration and exposure time. Relatively minor disturbances (maximum concentration 250 mg L^{-1}) decreased the organic content of periphyton after the first 24 hours of exposure. However, algal biomass (measured as chlorophyll *a*) was reduced only in the most prolonged exposure time (7 days). Periphytic nutrient stoichiometry (as indicated by molar organic C:N ratios) was not affected by sediment addition. Invertebrate drift was affected strongly by exposure time, and all taxa exhibited statistically significant responses within the first day under all concentrations. However, concentration interacted with exposure time in its effects on the drift of both mayfly species. The differing relative and interactive effects of concentration and exposure time demonstrate the importance of duration in the definition of disturbance effects and suggest that the common prediction of severity of effect based on a constant relationship between these two factors can produce considerable overestimates or underestimates of environmental risk.

Introduction

The disruption of natural disturbance regimes is a direct consequence of climate change, land use exploitation and many other human-induced changes to the environment from local (Yin and Li 2001, Allan 2004, Syphard *et al.* 2007) to global (Christensen and Christensen 2003, Lowe and Gregory 2005, Steffen *et al.* 2007) scales. The imposition of novel environmental conditions by humans is of central importance to ecological management and conservation (Chapin *et al.* 2000, Tilman and Lehman 2001). Understanding and anticipating the consequences of this relies on the capacity to identify the underlying mechanisms of action by which such changes are operating. Duration (*i.e.* the length of time a perturbation acts upon a system) is one of the principal constituent attributes of disturbances (White and Jentsch 2001) yet little work has been done to study its importance experimentally (but see Attayde and Hansson 2001, Bell *et al.* 2003, Hewitt and Norkko 2007). Of special interest is, however, the relationship between intensity and duration. This relationship is recognised as central to the definition of severity of effects in other biological disciplines such as toxicology (Doull and Rozman 2000, Rozman 2000). Toxicological studies with different contaminants have demonstrated that the individual effects of concentration and exposure time are not always additive and that their toxicity can depend strongly on their relative magnitude depending upon factors such as the mode of action of the toxicant, the possibility of bioaccumulation or the susceptibility of the exposed organism (*e.g.* Miller *et al.* 2000, Coman *et al.* 2005, Hoang *et al.* 2007). Given this, it is, therefore, likely that the specific combination of intensity and duration could be a key driver of the effects of environmental disturbances on ecosystems.

Sediment loads are a widespread major pollutant of surface waters worldwide and are the most important off-site impact of soil erosion (Pimentel *et al.* 1995, Waters 1995, Donohue and García Molinos 2009). Landscape alteration by human activities accelerates surface soil erosion by modifying basic components of the hydrologic cycle and increasing the amount of bare soil exposed to rainfall and runoff (Harr *et al.* 1975, King and Tennyson 1984, Chamberlin *et al.* 1991). The frequency and volume of mass erosion events also is linked strongly to the type and intensity of land alteration in the catchment (*e.g.* Rood 1984). Land clearance and changes in land use can increase catchment sediment yields by many orders of magnitude (Furniss *et al.* 1991, Nelson *et al.* 1991, Dearing and Jones 2003). The resulting large quantities of fine sediment are commonly delivered to stream channels with a frequency, timing, and duration that often differ from those of natural processes (Anderson *et al.* 1976, Ryan 1991, Wood and Armitage 1997). They can, thus, disrupt stream habitats and surpass the capacity of biota to withstand this otherwise natural component of streams (Waters 1995).

Both concentration (*i.e.* intensity) and duration comprise important factors in aquatic sediment risk assessment (Newcombe and McDonald 1991). Even relatively small concentrations of fine sediment can reduce autotrophic production (Davies-Colley *et al.* 1992), diminish algal organic content (Cline *et al.* 1982, Graham 1990, Yamada and Nakamura 2002), impair invertebrate feeding and growth (Broekhuizen *et al.* 2001, Peeters *et al.* 2006), enhance drift (Rosenberg and Wiens 1978), and promote changes in community composition and abundance (Culp *et al.* 1986, Suren and Jowett 2001). However, exposure time has generally been considered as a fixed arbitrary value or categorized to a specific duration range (*e.g.* acute, subacute, subchronic, or chronic). Such 'semiquantitative' categorization limits the applicability of test results because it

offers little insight into the relative individual effects of duration or of the possible existence of interactions between sediment concentration and exposure time. Shaw and Richardson (2001) reported reductions in invertebrate abundance and diversity and changes in the magnitude and composition of drift as sediment pulse duration increased. However, pulse concentration was constant in their experiment. Newcombe and collaborators (Newcombe and McDonald 1991, Newcombe and Jensen 1996, Newcombe 2003) have developed a number of predictive sediment dose-response models. These models are undoubtedly useful for management purposes. However, they focus exclusively on fish populations, and their calibration is based on a meta-analysis from data available in the literature obtained under different experimental conditions and peer consultation (Newcombe 2003).

Understanding the differential effects of toxic environmental pollutants requires specific knowledge of their concentration and exposure time and the pollutant-specific relationship between these factors (Mastin and Rodgers 2000, Murray-Gulde *et al.* 2002). Inherent in this task is the recognition of both factors as independent variables within the experimental design (Doull and Rozman 2000, Rozman 2000). I therefore established an experiment in which I quantified the individual and combined effects of sediment disturbances of different maximal concentration and duration on benthic algal biomass, proportional organic content, algal molar organic C:N ratios, and the survival and drift rates of stream macroinvertebrates. The purpose of the experiment was to test the hypothesis that ecological effects of disturbance depend on the specific combination of the intensity and duration of perturbations.

Methods

Experimental design

I established a fully-factorial experiment in laboratory-based artificial streams, where test organisms were exposed to sediment disturbances caused by the addition of different sediment loads (yielding maximum suspended solid concentrations of +0, +250, +600, and +2000 mg L⁻¹) over different durations (1, 3, 5, and 7 days). The experimental design consisted of two fixed factors (sediment concentration and disturbance duration) arranged orthogonally with four levels each (*i.e.* 16 treatments). Each treatment was replicated four times. Sixteen artificial streams were set up in four separated sets, each consisting of four units (Fig. 2.1A, B). Treatments were arranged randomly so that, for a given replicate run, each of the four sets was assigned one of the four sediment concentrations, and each of the artificial streams within the same set had a different exposure time (Fig. 2.1B). A set constituted a closed circuit in which unmodified river water was recirculated using a submersible pump from a collecting tank up to a feeding tank, then diverted equally by gravity into each of the 4 artificial streams in the set (Fig. 2.1A). Natural total suspended solid levels in the river water were very low with mean (\pm SE) values of 3.3 ± 0.4 mg L⁻¹. Outflows were conducted to the collecting tank by a gutter. A wire-mesh basket was installed at the outflow of each channel to collect drifting invertebrates.

Each pump provided a constant flow of approximately 1 L s⁻¹ and generated a current speed in each artificial stream of 5 ± 0.1 cm s⁻¹ and a depth that ranged from 31 mm at the head to 35 mm at the downstream end. Water temperature was kept at 8.2 ± 0.1 °C

throughout the experiment by coolers connected to the collecting tanks. Light was provided by fluorescent lights installed over the artificial streams and operated on a 14/10-h day/night cycle. Light intensity at the water surface level was 515 ± 14 lx (Rolinet® TES 1335 Digital Lux meter; Rotronic AG, Bassersdorf, Switzerland). The artificial streams had inner dimensions of 60 x 20 cm (1200 cm²), with beds made of stream material composed of cobbles (>64 mm), pebbles (16–64 mm), gravel (2–16 mm), and sand (<2 mm) in a respective volumetric ratio of 1:2:1:1.

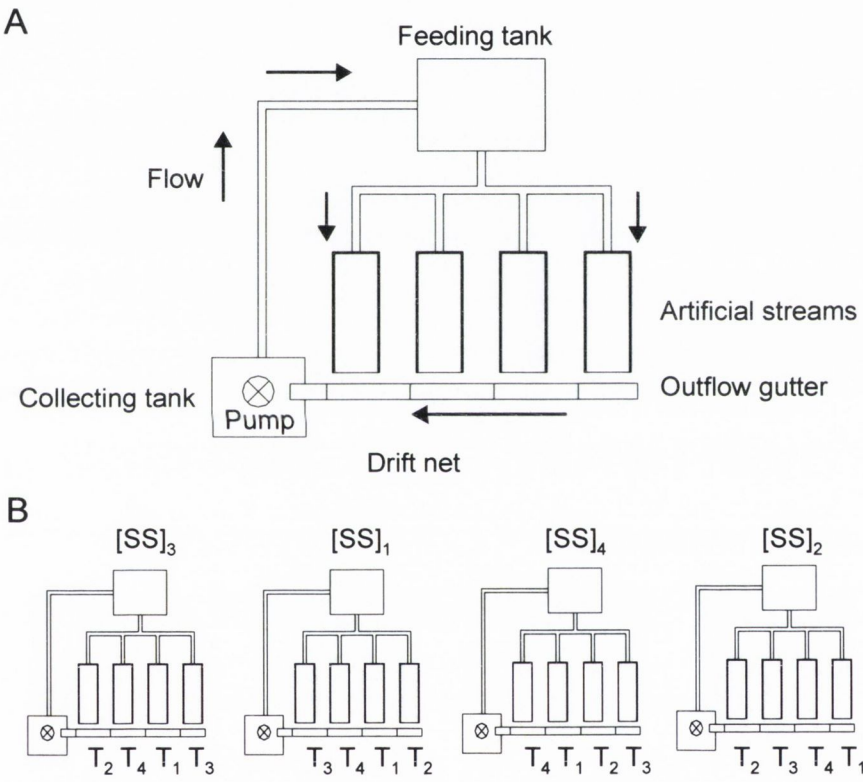


Fig. 2.1. (A) Design of the artificial stream sets (see *Experimental design* in Methods for explanation) and (B) example of distribution of suspended solid (SS) concentration and exposure time treatments (T) among experimental units.

Commercial topsoil (Kaloam®; Pitchcare.com Limited, Wolverhampton, UK) was oven-dried, ground mechanically, sieved through a 63 µm mesh, and ignited for 3 hours at 550°C. Disturbances were created by adding a preweighed quantity of fine sediment to three of the four experimental sets (+0 treatment excluded). Sediment loads were 1.08,

0.33, and 0.14 kg fine sediment m^{-2} of channel and yielded maximum suspended solid concentrations of +2000, +600, and +250 mg L^{-1} , respectively. The frequency of sediment addition was constant throughout the experiment and consisted of a single load every day at the same time to compensate for sedimentation within the artificial streams. Sediment loads were corrected for residual concentrations in the channels before addition. Vigorous manual stirring and the turbulence produced by the water falling from the collecting gutter provided adequate and rapid mixture of the sediment with the water. Recirculation of water ensured continuous homogeneous exposure of experimental organisms to suspended sediment. Sedimentation in the artificial streams was measured with sediment traps (62 cm^2 , one per channel) embedded at the same relative position in each stream unit. After completion of each exposure, collected sediment was oven dried at 60°C to constant mass and expressed as sedimentation rates ($\text{mg dry mass cm}^{-2} \text{ d}^{-1}$). Nutrient enrichment of water caused by the addition of sediment was quantified by measuring total P (TP) in each experimental treatment (following Eisenreich *et al.* 1975).

Before each replicate run, test organisms were collected from the Glencullen River at Eniskerry, Co. Wicklow, Ireland ($51^\circ 85.03' \text{ N}$, $3^\circ 12.86' \text{ W}$). Selection of invertebrate taxa and their abundances for the experiment was based on natural densities in the Glencullen River. A total of 160 individuals of *Asellus aquaticus* (L.), 160 of *Glossosoma boltoni* (Curtis), 96 of *Rhithrogena semicolorata* (Curtis), and 80 of *Baetis rhodani* (Pictet) was collected for each run, divided equally among the 16 stream units, and left overnight before sediment addition for acclimatization. Individuals that had drifted were reintroduced to the channels before the commencement of the experiment. Incomplete individuals (*i.e.* injured or without their case) were replaced. During the experiment,

invertebrate drift was recorded after the first 15, 30, and 60 minutes for the first day and on a 14- to 24-hour basis following a diel cycle. At the end of each replicate run, artificial streams were examined for any remaining macroinvertebrates. Casualties were recorded for both drifted and remnant individuals.

Three cobble-size stones (10–15 cm), also collected from the Glencullen River, were placed in each artificial stream at the beginning of each replicate run and used to quantify changes in the biomass (measured as chlorophyll *a*), proportional organic content, and organic C:N ratios of periphyton. Accretions on the upper surfaces of stones were collected with a brush and stored in polyethylene vials (<4°C) until analysis, which was always done within 24 h. Chlorophyll *a* concentrations were determined using methanol as extractant and ignoring degradation products (Standing Committee of Analysts 1983). Pigment concentrations were corrected for stone surface area, which was determined by wrapping the upper exposed surface of the stones in aluminium foil of known mass per unit area (Steinman *et al.* 2006). The autotrophic index (AI), expressed as the ratio between the periphytic organic matter (measured by loss on ignition, 3 hours at 550°C) and chlorophyll *a* content, was calculated as an indicator of the relative viability of the periphyton (Clesceri *et al.* 1999). Values exceeding the normal range of 50 to 200 indicate large accumulations of nonliving organic material (organic matter >> chlorophyll *a*) and, consequently, poor quality of the periphyton as a food source (Clesceri *et al.* 1999). Organic C and N concentrations of periphytic algae were quantified using a Carlo-Erba[®] model 252 elemental analyzer (LECO, St. Joseph, Michigan) after removal of inorganic C with sulphurous acid (Verardo *et al.* 1990).

Statistical analysis

Individual and interactive effects of suspended solid concentration and exposure time were tested with analysis of variance (ANOVA), with chlorophyll *a*, proportional organic content (% organic mass relative to sample dry mass), the AI, and molar organic C:N ratios as response variables. Analysis of the invertebrate drift data followed an identical model design, except that this analysis was based on Type II sum of squares, rather than on Type III sum of squares, as recommended by Langsrud (2003) for unbalanced designs. Invertebrate drift data were unbalanced because of the reduction in sample size over the length of the experiment (concentration: $n = 40$ throughout; exposure time: $n = 64$ on day 1 decreasing to $n = 16$ on day 7). Where a significant effect was detected, Tukey post hoc pair-wise comparisons were used to identify specific differences. The effects of fine sediment deposition on algal variables were examined with Pearson product-moment correlation analysis. Diel differences in total accumulated drift caused by suspended solid concentrations over the 7 day period were tested for each taxon by means of paired *t*-tests.

Observed values of each response variable were ranked from least to most affected, and response ranks were plotted against ranks of experimental treatment combinations ordered by dose (concentrations x exposure time) in an attempt to estimate qualitatively the usefulness of dose as predictor of treatment severity of effect on benthic organisms. The reasoning behind these graphs is that treatment ranks ordered by dose should match treatment ranks ordered by response if the effects of concentration and exposure time are additive or if the weights of both factors are similar (*i.e.* same individual effects).

Thus, ordered pairs of ranks should fall along a 1:1 line if dose calculated as the simple product of concentrations and exposure duration is a good predictor of severity of effect. All dependent variables were $\log(x)$ -transformed to meet assumptions of normality and/or homoscedasticity except for invertebrate drift rates, which were normalized based on the initial numbers of each taxon and $\log(1+x)$ -transformed. Statistical analyses were done with SPSS® Version 15.0 (Apache Software Foundation, Chicago, Illinois). Values for the response variables are given throughout as mean \pm standard error (SE).

Results

Despite the small size of the particles used in the experiment, sedimentation occurred in each of the sediment treatments. Initial mean turbidity levels after addition of sediment ranged from 134 ± 23 to 1051 ± 48 NTU depending on the treatment dose (+250 to +2000 mg L^{-1}). Deposition was initially very rapid, with reductions of *ca.* 65% of the initial concentrations occurring in all treatments within the first hour (Fig. 2.2). Over the 24 hour elapsed time between consecutive sediment additions, turbidity was reduced by *ca.* 97% of initial values. Sediment traps registered mean sedimentation rates in the artificial streams of 2.3 ± 0.1 , 6.5 ± 0.3 , and 20.5 ± 0.5 $\text{mg dry mass cm}^{-2} \text{ d}^{-1}$ for the +250, +600, and +2000 mg L^{-1} treatments, respectively. Deposition in the +0 treatments was below detection limits ($<0.1 \text{ mg cm}^{-2} \text{ d}^{-1}$).

Concentrations of water-column total P fluctuated considerably over the course of the experiment but generally increased with higher sediment concentrations and longer exposure times. Values ranged from $15.3 \pm 0.3 \text{ } \mu\text{g L}^{-1}$ (day 1) to $13.5 \pm 0.9 \text{ } \mu\text{g L}^{-1}$ (day 7) in

the +0 treatment up to $26.8 \pm 0.1 \mu\text{g L}^{-1}$ (day 1) to $167.6 \pm 1.8 \mu\text{g L}^{-1}$ (day 7) in the +2000 treatment.

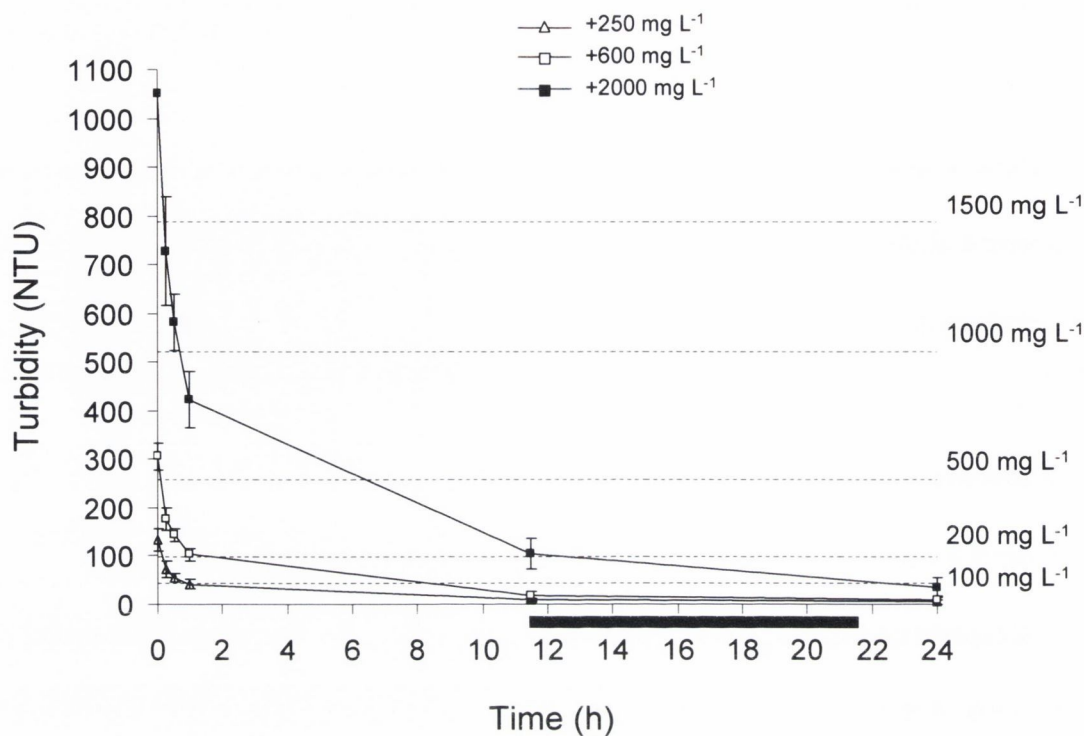


Fig. 2.2. Mean (\pm SE) turbidity in artificial streams in each sediment concentration treatment. Sediment was added once each day during the assigned exposure time (1, 3, 5, 7 days), and turbidity was measured 0.25, 0.5, 1, 11.5 and 24 hours after each addition. Horizontal lines indicate equivalent suspended solid concentrations. The bar along the x-axis indicates the night phase of the cycle.

Suspended solid concentration and exposure time did not interact significantly for any of the periphytic response variables measured (Table 2.1), so responses to treatments are described for each factor separately. Benthic algal biomass, expressed as chlorophyll *a*, decreased considerably across both concentration and exposure time gradients (Fig. 2.3A) but was affected significantly only by prolonged exposure times (Table 2.1). Benthic algal biomass differed significantly between days 1 and 7 (Tukey post hoc test, $p = 0.05$). In contrast, % organic content decreased significantly with both higher concentrations and longer exposure times (Table 2.1, Fig. 2.3B). Significant differences

were found among all sediment concentrations ($p < 0.05$) and between day 1 and each of the other exposure times ($p < 0.001$). Chlorophyll *a* and % organic content were reduced by $55.5 \pm 10.9\%$ and $94.7 \pm 1.5\%$, respectively, after 7 d in the +2000 treatment relative to levels on day 1 in the +0 mg L⁻¹ treatment.

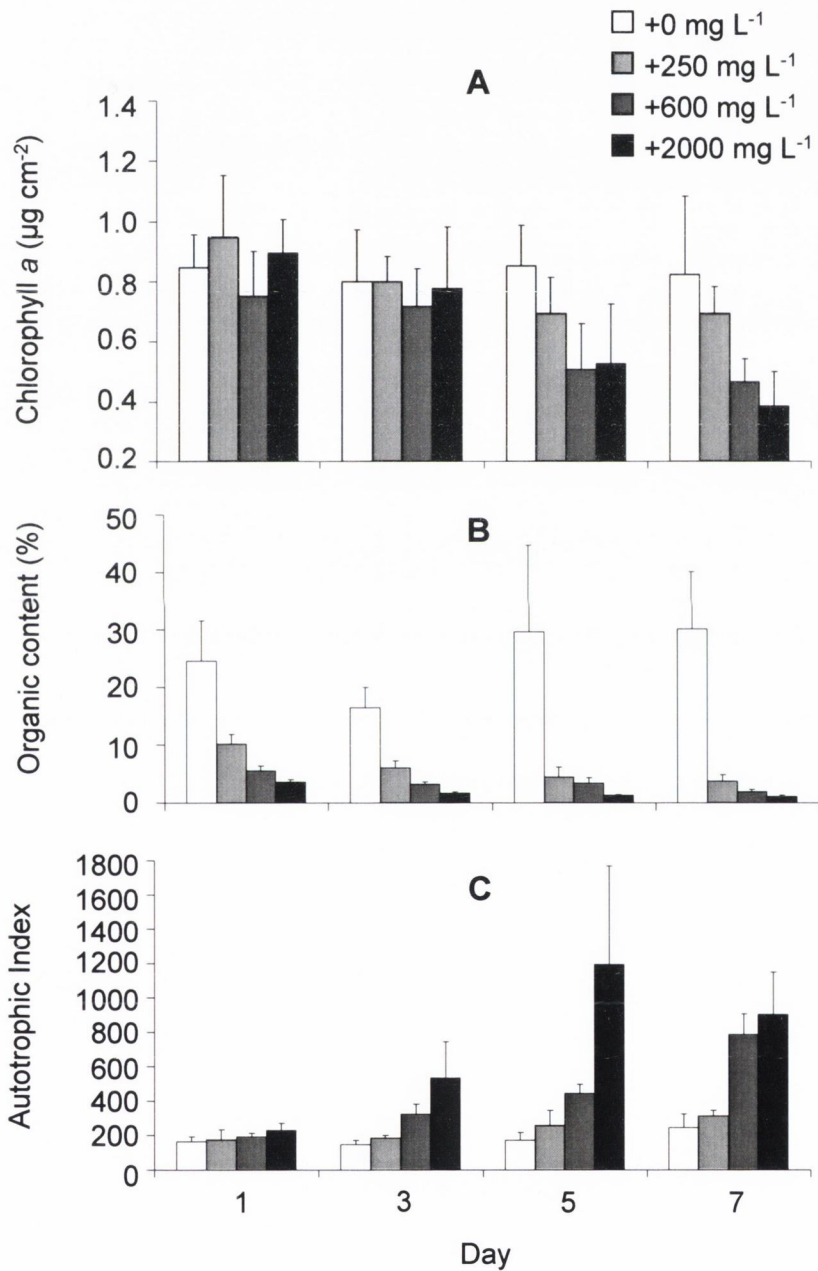


Fig. 2.3. Mean (\pm SE) (A) periphyton chlorophyll *a*, (B) organic content, and (C) autotrophic index for each sediment concentration x exposure time treatment combination.

Table 2.1. Results of ANOVA for effects of suspended solid concentration and exposure time on periphyton and macroinvertebrate drift. Periphytic variables were log-transformed and drift variables log(1+x)-transformed prior to analysis. Statistically significant effects are shown in bold font.

Variable	Treatment	df	MS	F	p
Periphyton					
<i>Chlorophyll a</i>					
	Concentration, C	3	0.12	2.5	0.07
	Exposure time, T	3	0.14	3.0	0.04
	C*T	9	0.02	0.5	0.84
	Residual	48	0.05		
<i>% organic content</i>					
	Concentration, C	3	3.5	85.3	<0.001
	Exposure time, T	3	0.36	8.7	<0.001
	C*T	9	0.07	1.7	0.12
	Residual	48	0.04		
<i>Autotrophic index</i>					
	Concentration, C	3	0.76	12.3	<0.001
	Exposure time, T	3	0.43	7.0	<0.001
	C*T	9	0.05	0.8	0.64
	Residual	48	0.06		
<i>C:N ratio</i>					
	Concentration, C	3	0.01	1.2	0.33
	Exposure time, T	3	0.002	0.2	0.88
	C*T	9	0.006	0.7	0.72
	Residual	48	0.009		
Macroinvertebrate drift					
<i>Baetis rhodani</i>					
	Concentration, C	3	0.02	6	0.001
	Exposure time, T	3	0.16	60.8	<0.001
	C*T	9	0.006	2.2	0.03
	Residual	144	0.003		

Table 2.1. Continued.

<i>Rhithrogena semicolorata</i>					
Concentration, C	3	0.02	8.6	<0.001	
Exposure time, T	3	0.12	49.2	<0.001	
C*T	9	0.008	3.3	0.001	
Residual	144	0.002			
<i>Asellus aquaticus</i>					
Concentration, C	3	0.0004	0.4	0.78	
Exposure time, T	3	0.12	102.1	<0.001	
C*T	9	0.0003	0.2	0.99	
Residual	144	0.001			
<i>Glossosoma boltoni</i>					
Concentration, C	3	0.0003	0.2	0.9	
Exposure time, T	3	0.04	19.2	<0.001	
C*T	9	0.001	0.5	0.84	
Residual	144	0.002			

AI increased significantly with both higher concentrations and longer exposure times and was five times greater in the +2000 mg L⁻¹ and 7 day treatment (901.9 ± 246.8) than in the +0 mg L⁻¹ and 1 day treatment (166.8 ± 27.6) (Table 2.1, Fig. 2.3C). Values exceeded 200 by the first, third and fifth day in the +2000, +600, and +250 mg L⁻¹ treatments, respectively. Significant differences ($p < 0.05$) were found among all sediment concentrations except between the two lowest and the two highest concentrations. Values also differed significantly among all exposure times ($p < 0.05$), except for treatment pairs differing by a single exposure time level (*i.e.* days 1–3, 3–5, and 5–7). No significant effect of concentration or exposure time was found on periphytic molar organic C:N ratios (Table 2.1), which ranged between 6.12 and 7.98 regardless of concentration or exposure time levels. Sediment deposition was correlated inversely with chlorophyll *a* concentration ($r_{63} = -0.40$, $p < 0.001$) and the % organic matter content of periphyton ($r_{63} = -0.91$, $p < 0.001$), and positively with AI ($r_{63} = 0.67$, $p < 0.001$).

No macroinvertebrate taxon showed an instant response to the addition of sediment. Total drift numbers during the first hour following addition of the sediment were very low and did not show any specific trend either within or among taxa, even at the highest concentration level (Fig. 2.4A–D). Drift numbers for all taxa registered a clear peak after 24 hours of exposure. Drift numbers were consistently lower for the remainder of the experiment. Differences in drift rates attributable to exposure time were highly significant for all taxa (Table 2.1). Significance consistently corresponded to differences between day 1 and the three other exposure times ($p < 0.001$).

Sediment concentration produced significant relative and interactive effects with exposure time on drift of the mayflies *B. rhodani* and *R. semicolorata* (Table 2.1). Drift under the two higher concentrations (+600/+2000 mg L⁻¹) was significantly higher than that under the two lower concentrations (+0/+250 mg L⁻¹; $p < 0.05$). The mayflies were the two most sediment-sensitive taxa in the experiment (as indicated by tendency to drift) and constituted >40% of the initial numbers drifted after day 1 in the +600 (44 ± 5% *B. rhodani*, 41 ± 5% *R. semicolorata*) and +2000 mg/L (55 ± 5% *B. rhodani*, 48 ± 4% *R. semicolorata*) treatments (Fig. 2.4E, F). Drift numbers of *G. boltoni* and *A. aquaticus* were not affected significantly by either concentration or its interaction with exposure time (Table 2.1). *Glossosoma boltoni* had the smallest response to sediment addition, and >30% of the initial numbers remained in all concentrations after day 7 (Fig. 2.4H). *Asellus aquaticus* drifted more in the +0 sediment treatment than in sediment-addition treatments, a response that was accentuated progressively with increasing exposure time (Fig. 2.4G). By day 7, 73 ± 10% of the initial numbers had drifted in the +0 sediment treatment, whereas ca. 50% of initial numbers had drifted in the rest of the treatments.

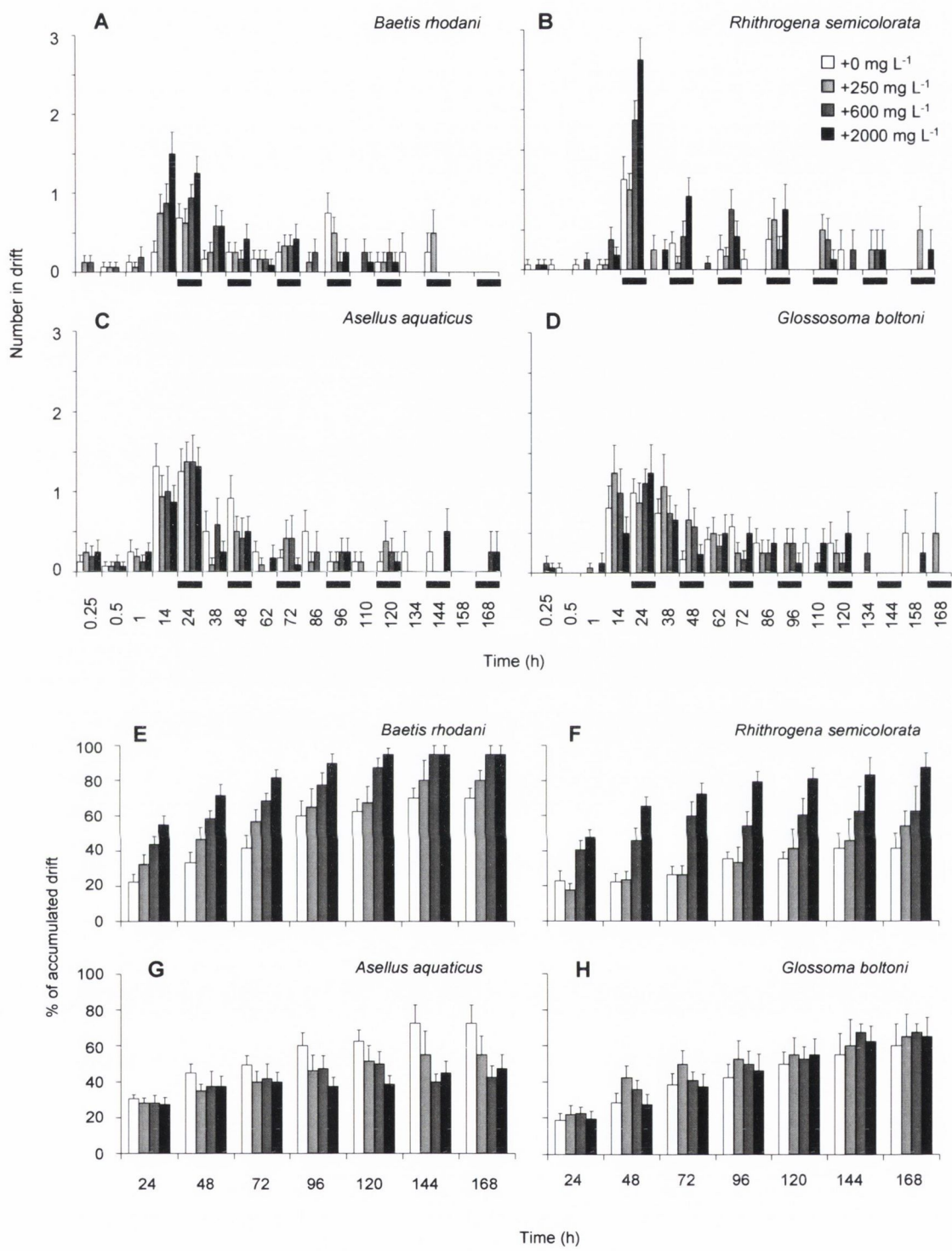


Fig. 2.4. Mean (\pm SE) number of drifting (A) *Baetis rhodani* (initial $n = 5$ per channel), (B) *Rhithrogena semicolorata* ($n = 6$), (C) *Asellus aquaticus* ($n = 10$), and (D) *Glossosoma boltoni* ($n = 10$), and % of accumulated drift relative to initial n of (E) *B. rhodani*, (F) *R. semicolorata*, (G) *A. aquaticus*, and (H) *G. boltoni* as a function of suspended solid concentration and exposure time. Bars along the x-axis indicate the night phase of the cycle. Number of samples decreases with exposure time (1 day, $n = 16$; 2-3 days, $n = 12$; 4-5 days, $n = 8$; 6-7 days, $n = 4$).

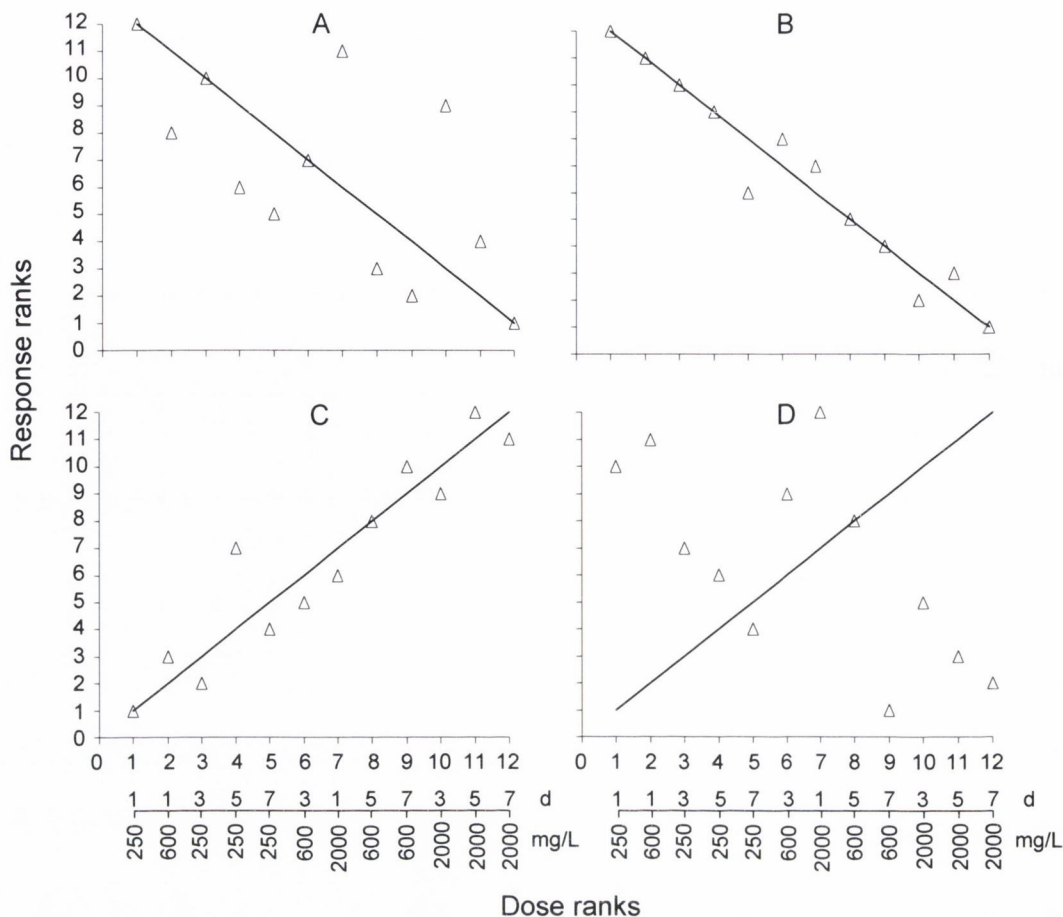


Fig. 2.5. Treatments ranked by sediment dose (concentration x exposure time) against mean (A) chlorophyll *a* concentrations and (B) % organic content of periphyton, (C) the autotrophic index, and (D) total invertebrate drift. Lines show rank relationship expected under the assumption of equality of effect between concentration and exposure time. Departures from the line indicate underestimations or overestimations of the effect derived from this assumption.

Accumulated drift numbers at the end of the experiment showed no significant diel pattern for any of the experimental taxa except for *R. semicolorata*, which drifted significantly more at night across all concentrations (paired *t*-test; +0, $t_3 = -3.4$, $p = 0.043$; +250, $t_3 = -5.0$, $p = 0.015$; +600, $t_3 = -3.6$, $p = 0.037$; +2000, $t_3 = -7.4$, $p = 0.005$). Survival was very high among all species and in all treatments. Only one *G. boltoni* and 15 *A. aquaticus* died from all treatments over the course of the experiment (640 individuals).

Rank ordination of the experimental treatments by dose (concentration x exposure time) against the observed values showed distinct patterns depending on the response variable under consideration (Fig. 2.5A– D). Though the lowest ($+250 \text{ mg L}^{-1} \times 1 \text{ d}$) and the highest ($2000 \text{ mg L}^{-1} \times 7 \text{ d}$) doses corresponded to the highest ($0.95 \mu\text{g cm}^{-2}$) and lowest ($0.38 \mu\text{g cm}^{-2}$) chlorophyll *a* concentrations, respectively, departure from the expected rank order of severity of effects based on overall treatment dose was clear (Fig. 2.5A). Qualitative overestimation of the effect (*i.e.* higher rank than expected) generally corresponded to combinations of short exposure times and high concentrations ($+2000 \text{ mg L}^{-1} \times 1 \text{ day}$: +5 ranks; $+2000 \text{ mg L}^{-1} \times 3 \text{ days}$: +6 ranks), whereas underestimations were associated strongly with prolonged exposure times and low or moderate concentrations ($+250$ or $+600 \text{ mg L}^{-1} \times 5$ or 7 days). However, organic matter and Al ranks appeared clustered near the theoretical response line, a result that indicated a close relationship between overall dose and response (Fig. 2.5B, C). Invertebrate drift ranks were, however, scattered widely. Departures from the theoretical response line were driven by the strong drift response shown by all taxa after the first 24 hours of exposure time (Fig. 2.5D). Treatments linked to short exposure times were associated with large underestimations of effect, whereas treatments linked to long exposure times had much lower observed ranks than expected.

Discussion

My results demonstrate that ecological responses to disturbance can be driven by the specific combination of the intensity and duration of perturbations. The varying combined effects of sediment concentration and exposure time over the experiment suggest strongly that the relationship between these factors can be additive or

synergistic depending upon the response variable under consideration. Further, sediment concentration and exposure time had different relative effects on different response variables. Reductions in the percent organic content of periphyton were observed after the first 24 hours even under the lowest sediment concentration ($+250 \text{ mg L}^{-1}$). Effects were exacerbated by the active deposition of sediment particles, as indicated by the strong inverse correlations of concentration with algal biomass and % organic content. However, algal biomass was limited only by prolonged exposure times, regardless of concentration, although concentration effects were bordering on significance. This suggests that, within the range of exposure times and concentrations tested, the duration of light deprivation might have been a more influential factor for algal populations than the proportion of light attenuated. The relative enrichment of the water with P associated with sediment addition may have ameliorated to some extent the negative effects of increasing sediment concentrations and exposure times (Burkholder and Coker 1991). Nutrient availability does not appear, however, to have been a confounding factor in terms of limiting algal growth given the observed general stability of molar organic C:N ratios in all treatments (6.1–8), which were well within the optimum periphyton stoichiometric range of 5 to 10 (Hillebrand and Sommer 1999). These results concur with the concept that C:N ratios are stable against changes in abiotic conditions (*e.g.* light limitation), and suggest that neither N nor P were limiting growth for periphyton (Goldman 1986, Hillebrand and Sommer 1999).

Exposure time, concentration, and their interaction generated different responses in terms of invertebrate drift. In a temporal context, drift was clearly driven by the short-term response exhibited by all taxa within the first 24 hours, which was likely responsible for the highly significant differences in effects of exposure time among

treatments. However, the absence of an immediate drift response during the first hour following the initial addition of sediment even under the highest concentration was remarkable. Enhanced drift as a response to elevated mineral turbidity has been observed frequently in field and laboratory studies (Pearson and Franklin 1968b, Doeg and Milledge 1991, Bond and Downes 2003) and has been attributed either to catastrophic drift produced by scouring under high-flow conditions or to behavioural drift caused by a reduction in light reaching the stream bed. However, in my experiment, the absence of an initial response and the peak in drift observed later for all taxa suggests the operation of other mechanisms. Rapid reduction in water column turbidity from high sedimentation rates together with the shallow nature of my artificial streams may have allowed sufficient light penetration to inhibit light-driven drift. Ciborowski *et al.* (1977) observed that drift levels of mayfly nymphs increased only during dark periods and not immediately following addition of sediment. They concluded that organisms probably reacted to deposited sediment rather than to its suspended fraction because the Plexiglas sides of the laboratory stream allowed substantial light penetration.

Significant interactions between concentration and exposure time on mayfly drift could have resulted from a combination of factors derived from the deposition and accumulation of fine sediment, such as homogenisation of the substrate and interstitial habitat reduction (Ciborowski *et al.* 1977, Lenat *et al.* 1981, Hubert *et al.* 1996, Suren and Jowett 2001, Bo *et al.* 2007, Connolly and Pearson 2007), attachment or movement limitation (Ryan 1991, Wood and Armitage 1997), and, in the case of *Rhithrogena*, reductions in periphyton food availability and nutritional value (Hildebrand 1974, Brittain and Eikeland 1988, Graham 1990, Broekhuizen *et al.* 2001, Suren and Jowett 2001, Peeters *et al.* 2006). Unexpectedly, *G. boltoni* showed a much milder increase in

drift across exposure times and the lowest variability among concentrations despite having habitat requirements similar to those of *Rhithrogena* and the fact that they feed on periphyton (Hynes 1970). The greater (and less costly energetically) mobility of *Rhithrogena* relative to the crawling of *Glossosoma* may have resulted in greater drift as available clear food patches became scarcer because of sedimentation; increased activity when searching for food at low resource levels have been shown to increase the drift of *Rhithrogena* (Hildebrand 1974). It is, however, also possible that the two species entered into resource competition as the periphyton became increasingly silted. The high feeding efficiency of *Glossosoma* generally makes it a dominant consumer at low food resource levels (Kohler 1992). The ratio of algae to loose material ingested by scrapers is essentially a function of the relative densities of both materials within patches of periphyton (Cummins 1975), but increased feeding rate could compensate for decreased nutritional value of the consumed food (Cummins and Klug 1979). Further, the biofilms that commonly grow upon clays and sands may have provided a nutritional supplement (Lind and Davalos-Lind 1991, Lind *et al.* 1997, Broekhuizen *et al.* 2001). Differences in feeding-appendage morphology may otherwise influence the ability to scrape and brush algae from silted stones (scoop-shaped mandibles with a cutting edge of *Glossosoma* as opposed to the stout bristles of the labial and maxillary palps of *Rhithrogena*).

The apparent inhibitory effect of sediment deposition on the drift of *A. aquaticus* may be attributable to the increasing quantities of fine particulate organic matter accumulated under increasing sediment loading, as indicated by AI values. *Asellus* can colonize reaches with abundant fine sediments where it functions as a facultative collector-gatherer feeding on decomposing fine particulate organic matter (Merritt and Cummins

2006). Extence (1978) reported increased abundances of *A. aquaticus* in the River Roding (Essex, Great Britain) as a result of fine sediment deposition from motorway construction works.

My results and those of other sediment-manipulation experiments (e.g. Suren and Jowett 2001, Matthaei *et al.* 2006, Peeters *et al.* 2006, Bo *et al.* 2007) and field studies (e.g. Lemly 1982, Davey *et al.* 1987, Fritz *et al.* 1999, Wood and Armitage 1999, Zweig and Rabeni 2001, Yamada and Nakamura 2002) indicate that increased sediment loading of stony stream habitats under low-flow conditions strongly affects benthic biota through siltation of the stream bed, despite initially high concentrations of suspended solids. In the absence of an immediate response from the benthic fauna (*i.e.* catastrophic drift), short-term effects of sedimentation include increased behavioural drift (Ciborowski *et al.* 1977, Suren and Jowett 2001) and considerable reductions in benthic algal availability and quality as a food resource because of entrapment and accumulation of fine sediment within the algal matrix (Graham 1990, Yamada and Nakamura 2002). Reductions in algal biomass (chlorophyll *a*) tend to be relatively delayed and are the consequence of reduced light reaching the stream bed (caused by suspended particles) and the shielding effect of the deposited sediment layer (Davies-Colley *et al.* 1992, Suren and Jowett 2001). The very low mortality rates of invertebrate taxa in my experiment, even under the highest concentration and longest exposure time, are indicative of a capacity to survive in silted environments for relatively short periods of time although biological impairment is expected. Peeters *et al.* (2006) found high survivorship among *Heptagenia sulphurea* mayfly larvae cultured in silted aquaria after 37 days (particle size <1 mm), but they observed significant reductions in growth in relation to controls. Therefore, behavioural drift is likely to override mortality as the major causal factor

producing short term reductions of standing crops in silted environments. Finer fractions of deposited sediment (silt and clay) produce more rapid and severe effects on benthic fauna in the short term (*e.g.* Doeg and Koehn 1994, Donohue and Irvine 2003) than do coarser particles, such as sand (*e.g.* Culp *et al.* 1986, Bond and Downes 2003).

Extrapolation of my findings to natural conditions has important practical implications for conservation and management. My results demonstrate that the nature and strength of the relationship between disturbance intensity and duration may vary substantially depending upon the biological component under consideration. A common method for predicting the severity of effect of a pollutant is to assume that dose, the product of concentration and exposure time, produces a constant level of effect for a given end point [*i.e.* variation in concentration or exposure time does not affect the resulting effect, providing dose remains constant, also known as 'Habers rule' (Haber 1924)]. However, this rule cannot hold if the relative weights of both variables differ or if concentration and exposure time interact (Gardener *et al.* 1979, Miller *et al.* 2000). Under the assumption of equality of weights between concentration and exposure time, we would expect the severity of effect to increase (or decrease) consistently with sediment dose. This was not the case in my study. Rank correspondence between dose and observed values was strongly variable-specific. Rank correspondence was stronger for those variables for which significant differences were caused by both concentration and exposure time (% organic matter content and AI) than those variables for which differences were driven more by one factor than the other (chlorophyll *a* and drift). This result reflects the existence of differential relative effects. Therefore, important overestimates or underestimates of effects (and consequently risks) can be made by using overall dose as a predictor. This result suggests strongly that the environmental

risk associated with anthropogenic disturbances can be defined accurately only by considering both relative and combined contributions of intensity and duration to levels of effect. Future research will benefit from inclusion of the effects of multiple levels of duration and intensity in experimental disturbance studies to yield intensity-duration-response data from which dose-response models can be calibrated, tested, and improved.

Chapter III. The temporal pattern of intensity within perturbation events regulates the effects of disturbances.



General upstream view of experimental set up (Photo by Jorge García Molinos)

In the previous chapter, I demonstrated how the specific combination of the intensity and duration of perturbations mediated sediment disturbance effects on stream benthic biota. Here, I use flow-through channels in the field to investigate experimentally how the temporal pattern of disturbance within sediment perturbations (which was independent of their duration, mean intensity, timing and frequency) affects the biota of a headwater stream.

Abstract

Disturbances are inherently variable in both time and space. This heterogeneity comprises a key determinant of ecosystem responses. Temporal patterns of disturbance can, however, vary significantly both within and among individual perturbations. While recent work has demonstrated the importance of variability among perturbations, previous work investigating the effects of temporal variability within perturbations has consistently confounded temporal variability with other disturbance attributes (*e.g.* overall intensity, frequency, duration or extent). The effects of temporal variability in intensity within individual perturbation events remain, therefore, unknown. I established a field experiment to test the hypothesis that the temporal pattern of intensity within perturbation events can drive the responses of ecosystems to disturbance. I did this by examining the effects of two sediment disturbance regimes comprising individual perturbations of contrasting temporal pattern (constant and temporally variable intensities) on the benthic invertebrate assemblage of a headwater stream. The duration, overall intensity, timing and frequency of the perturbations were, however, identical. I found that invertebrate drift during the temporally variable disturbances was greater and differed in taxonomic and trophic structure than that caused by the constant disturbances. The temporal pattern within perturbations had, however, no effect on benthic invertebrate assemblages *in situ* immediately after cessation of disturbances. The addition of sediment *per se* reduced both the abundance and diversity of invertebrate assemblages and altered their composition and trophic structure. However, I found that benthic assemblages exposed to the constant perturbations took longer to recover than those exposed to temporally variable perturbations. My results therefore demonstrate that variability in the temporal pattern

of intensity within individual perturbations can be an important driver of ecosystem responses to, and recovery from, disturbances. Temporal variability of sediment disturbances regulated, independently of other disturbance attributes, not only the extent of biotic responses but also determined the nature of those responses. The use of the absolute values such as the mean or maximum intensity of perturbations to define ecosystem health risks, therefore, ignoring potentially highly important information that may result in ineffective or inappropriate management decisions. Effective environmental management and policy necessitate the collection of data on the temporal patterns of intensity both within and among perturbations.

Introduction

Research into the effects of disturbances on ecosystem processes has a well-established central role in ecology (*e.g.* Dayton 1971, Connell 1978, Sousa 1984, Platt and Connell 2003, Shea *et al.* 2004). Disturbances are a major source of temporal and spatial heterogeneity in natural communities and constitute a key driver of natural selection (McAuliffe 1984a, Ostrander *et al.* 2000, Wilson and Tilman 2002, Bracken *et al.* 2008). The transformation of the environment by human activities tends, however, to operate at faster rates and over larger scales than most natural disturbances, compromising the stability of the biosphere by altering its most fundamental processes (Vitousek 1994, Vitousek *et al.* 1997, Vörösmarty and Sahagian 2000). The consequences of this are not only of great ecological concern (Chapin *et al.* 2000, Thomas *et al.* 2004) but also have considerable implications for human welfare (Costanza and D'Arge 1997, Chapin *et al.* 2000, Zhang *et al.* 2007). Understanding and planning for the ecological impacts of disturbances constitutes, therefore, an urgent necessity for scientists, managers and policy makers alike (Mintzer 1992, Lubchenco 1998, Omann *et al.* 2009).

One of the biggest challenges for the study of disturbance comprises the high degree of spatial and temporal variability inherent both within and among perturbations (White 1979, Sousa 1984, Pickett and White 1985, White and Jentsch 2001). This heterogeneity can result in high variability in ecosystem responses (Benedetti-Cecchi 2003, Fraterrigo and Rusak 2008). Different aspects of disturbance regimes, including their frequency (*e.g.* McCabe and Gotelli 2000, Heather *et al.* 2008) and duration (*e.g.* Marshall and Bailey 2004, García Molinos and Donohue 2009) have commonly been used in perturbation experiments to define their temporal pattern. For practical purposes, the temporal

variability associated with a disturbance regime can be partitioned in two components; heterogeneity in the distribution of perturbations over time and that embodied within individual perturbation events (Fig. 1). With the exception of some early studies (*e.g.* Robinson and Sandgren 1983), experimentation into the effects of temporal variability among perturbations has been traditionally approached by the use of disturbance frequency. However, the adequacy of frequency as a descriptor of temporal variability is limited by the fact that varying the frequency of disturbances alters both the number of events per time and the overall intensity associated with the disturbance regime. This prompted Benedetti-Cecchi (2000, 2003) to propose a new framework for the experimental analysis of the spatiotemporal variance of disturbance processes, prompting further research into the subject (Bertocci *et al.* 2005, Benedetti-Cecchi *et al.* 2006, Atalah *et al.* 2007, Cifuentes *et al.* 2007, Wollgast *et al.* 2008). Characterization of the temporal pattern of individual perturbations in experimental disturbance ecology has traditionally been based on disturbance duration (Bender *et al.* 1984, Glasby and Underwood 1996), typically involving a contrast of prolonged (press) versus discrete (pulse) perturbations (*e.g.* Marshall and Bailey 2004). However, these studies do not provide insight into the possible biotic effects derived from variable patterns of intensity within perturbation events, something common to most types of human and natural disturbances (*e.g.* Swanston 1991, Schwikl 2003, Poff *et al.* 2006, Banas *et al.* 2008, Crosa *et al.* 2010). Both theoretical (*e.g.* Lake 2000, 2003) and empirical (*e.g.* Poff and Ward 1989, Richter *et al.* 1996, Fritz and Dodds 2005, Sabo and Post 2008) studies have recognized the importance of temporal variability in intensity within individual disturbance events. However, few experimental studies have investigated its ecological implications, usually comparing gradual versus abrupt pressed (*e.g.* Klironomos *et al.* 2005) or pulsed (*e.g.* Imbert and Perry 2000) changes. These studies have demonstrated

that effects of abrupt changes are normally more severe than those of gradual changes because they can exceed the adaptation or tolerance capacity of exposed organisms. A consistent problem with these experiments, however, is that the effects of temporal variability in intensity were confounded with those of other disturbance traits. For example, Imbert and Perry (2000) studied the effect of gradual versus abrupt flow increases on stream macroinvertebrates. However, by fixing both treatments to reach equal peak flows with similar overall intensities they differed in duration. Similarly, Irvine and Henrique (1984) set flood pulses to be of equal duration but the differences in rate of change made the intensity differ by several orders of magnitude among treatments.

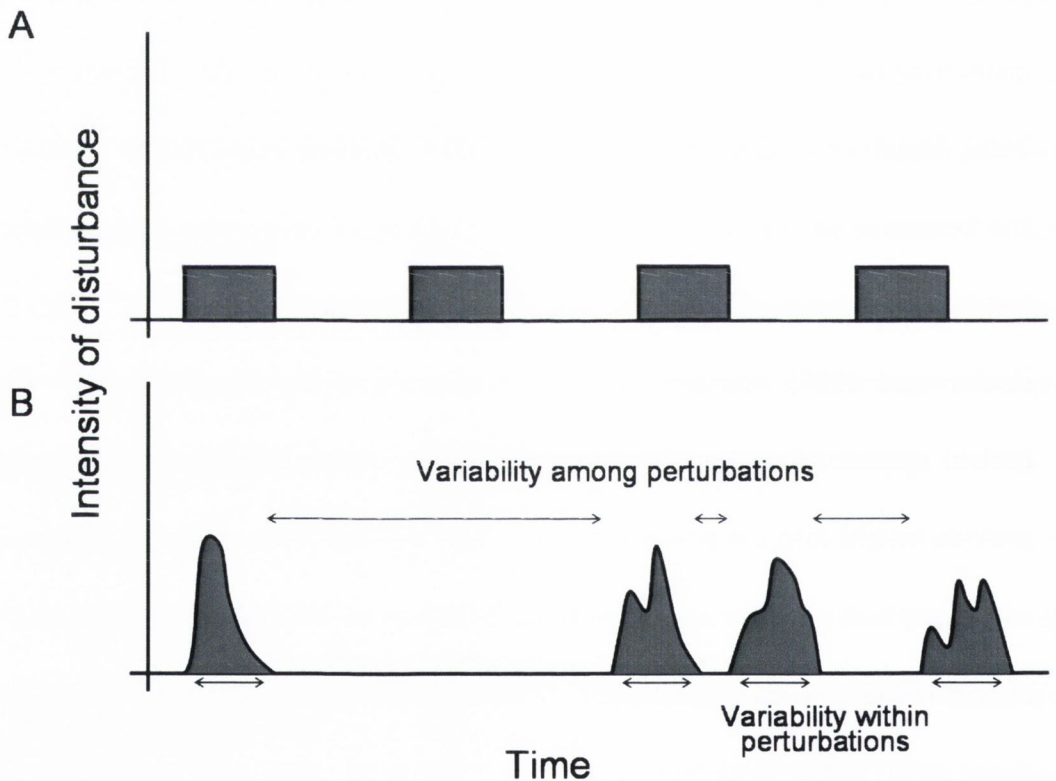


Fig. 3.1. Schematic representation of (A) a disturbance regime with no temporal variability and (B) an equivalent regime in terms of disturbance duration, mean intensity and frequency with temporal variability occurring both within and among perturbations.

High variability in intensity within perturbations can cause rapid and abrupt changes in the strength of disturbances compared with more constant processes even when their

overall mean intensity and duration remains the same (Fig. 1). Such variability, common to most types of natural and anthropogenic disturbances is known to alter environmental conditions by modifying, for example, pollutant availability (e.g. Zhang et al. 1997, Potter et al. 2006). The temporal pattern of perturbations could, thus, be important in driving the responses of ecosystems at different levels of ecological organisation if such variability alters the capacity of the disturbed system to withstand and recover from the disturbance. Quantification of the effects of varying temporal patterns of intensity within individual perturbation events, unconfounded with those of other disturbance traits, is therefore essential, both to support existing knowledge and to attain a mechanistic understanding of the effects of the temporal pattern of disturbances on ecosystems.

I tested experimentally in the field the hypothesis that the temporal pattern of intensity within perturbations drives the responses of biological communities to disturbance. My experimental site comprised a headwater stream in which I quantified the effects of two contrasting sediment disturbance regimes composed of individual perturbations differing in temporal pattern (constant versus temporally variable sediment loading) on benthic invertebrate assemblages and on their subsequent recovery. Increased sediment loading is recognised as one of the most widespread and pervasive anthropogenic disturbances of aquatic ecosystems (Wood and Armitage 1997, Donohue and García Molinos 2009). To unconfound the effects of temporal variability within perturbations from those of other disturbance traits, the frequency (number of perturbations per unit time), mean intensity (strength of disturbances), duration and process stochasticity (time elapsing between consecutive disturbances) of perturbations were equal across all disturbed treatments.

Methods

Experimental design

I established my field experiment in a uniform riffle reach of the River Liffey (County Wicklow, Ireland; 53°09.72'N, 06°22.13'W), approximately 6.5 km from its source in the Wicklow Mountains. At this point, the river is a third-order stream (approximately 12 m in width) exposed to minimal anthropogenic disturbance. The study reach had little riparian canopy and was characterised by relatively uniform bed morphology dominated by gravel, cobbles and boulders. The water depth across the site over the duration of the experiment ranged between 0.1 and 0.4 m.

I tested the effects of varying temporal patterns of disturbance within perturbation events on stream benthic invertebrate assemblages by creating two distinct sediment disturbance regimes using in-stream flow-through channels. One regime comprised 'press' pulses where a constant sediment dosage was maintained for the duration of the disturbances (constant treatment), while the second disturbance regime was defined by 'ramped' pulses, with dosage decreasing consistently over the total length of the disturbances (variable treatment). Ramped pulses are common in sediment disturbances resulting from anthropogenic activities such as effluent discharge and extractive operations (Pentz and Kostaschuk 1999, Krishnaswamy *et al.* 2006, Banas *et al.* 2008). Both regimes were applied over five days and had otherwise constant frequency (one perturbation every 24 hours) and were composed of disturbances of the same mean intensity ($12 \text{ kg soil h}^{-1}$) and duration (3 hours). My experimental treatments were completed by procedural controls (undisturbed channels) and, where possible, a control

reach outside the channels located in a structurally similar riffle located 30 m upstream from the experimental reach. Allocation of treatments to the experimental units was done randomly with three replications per treatment.

Nine bottomless channels (2.5 m long x 0.4 m wide x 1.0 m high), ballasted with boulders, were placed onto the experimental site taking care to avoid disturbance of the stream bed. Sieved (<2 mm) top soil was combined with stream water in circular 450 L tanks and supplied to the channels by gravity via valve-regulated polyvinyl chloride pipes connected to the upstream end of the channels. Sediment particles inside the tanks were kept in suspension by continuous recirculation of the water with a submersible pump and manual stirring. Mean particle-size composition (Mastersizer 2000[®] particle size analyzer, Malvern Instruments Ltd, Worcestershire, UK) of the sediment (\pm SD, $n = 10$) supplied to the channels was 62 ± 21.8 % silt and clay (<63 μm), 19.2 ± 12.2 % fine sand (63 μm -0.125 mm), 15.7 ± 10.5 % medium sand (0.125 mm-0.5 mm) and 2.2 ± 0.9 % coarse sand (0.5-2 mm). Organic matter content in the sediment, determined by loss on ignition (24 hours at 60 °C followed by 3 hours at 550 °C), was 3.3 ± 0.4 %. Sediment disturbances were repeated for 5 days at the same time each morning in May 2008. Subsequent recovery of biotic assemblages was then assessed 5 and 12 days after the final experimental disturbance.

Sampling and laboratory analyses

Water turbidity was quantified (2100P HACH[®] turbidimeter, Loveland, Colorado, USA) from the middle section of each channel every 20 minutes during disturbances. Water samples were also taken from the same location to quantify total suspended solids (TSS)

in the water column. One sample for quantification of TSS was taken every day from the control channels during disturbances, two from the constant treatment channels (before and during disturbances), and three from the variable treatment channels (before, beginning and end of disturbances). Samples were stored in the dark at less than 4°C and returned to the laboratory for analysis following standard methods (Clesceri *et al.* 1999). Sediment traps (0.12 m long x 0.22 m wide) were placed randomly in the downstream end of each channel to measure sedimentation rates. Traps were removed after completion of the last addition of sediment, their content dried (40 °C) to constant mass and sieved to determine fine sediment (<2 mm) mass.

Nets (0.4 x 0.4 m, 500 µm mesh) attached to the outlet of each channel were used to quantify invertebrate drift. Drift was measured both before and after sediment addition over the five days of experimental disturbance to account for possible direct (immediate drift; occurring during each 3 hour disturbance) and indirect (delayed drift; integrated over the 21 hours between consecutive disturbances) responses to treatments. My attempts at placing drift nets at the upstream control site failed owing to unstable nature of the stream bed. Therefore, there was no treatment controlling for any effect of the experimental channels on invertebrate drift. In addition to invertebrate drift, the composition and abundance of benthic invertebrate assemblages *in situ* were also quantified immediately (Day 5 of the experiment) and 5 (Day 10) and 12 (Day 17) days after the final disturbance (Fig. 3.2A). These samples, taken from random locations within each experimental channel and from the upstream control reach, were collected with a modified Hess sampler which enclosed 707 cm² of substrate (0.30 m diameter, 250 µm mesh). All invertebrate samples were sieved through a 500 µm sieve and preserved on site in ethanol. Invertebrates were then sorted in the laboratory and

identified to the lowest taxonomic level practicable. Collected taxa were also assigned to functional feeding groups (FFGs) following Merrit and Cummings (1996).

Concurrent samples of periphyton were collected on each date to assess treatment effects on algal biomass. Three smooth cobbles (10-20 cm) were taken from each channel prior to the collection of invertebrate samples. Accretions on stone upper surfaces were brushed off with a hard-bristle brush on a plastic tray containing a small quantity of river water. The samples were then pooled in a polyethylene bottle and stored in the dark at less than 4°C for transport back to the laboratory. Two 50 ml aliquots were taken for analysis of periphytic chlorophyll *a* and organic matter (ash free dry mass; AFDM) following standard procedures as described previously (Chapter II in this Thesis). Because AFDM incorporates all sources of organic matter (autotrophic, heterotrophic and non-living), it is regarded as a coarse measure of algal biomass (Steinman *et al.* 2006). Chlorophyll *a* concentrations were used, therefore, as an indicator of periphytic biomass. The ratio of total to autotrophic biomass (autotrophic index; AI = AFDM/chlorophyll *a*) was used, however, as an indicator of the relative viability of the periphyton (Clesceri *et al.* 1999).

Statistical analysis

The effects of varying temporal patterns within perturbations on periphytic variables, and the abundance and taxon richness of invertebrate drift and benthic assemblages *in situ* were analysed with repeated measures analysis of variance (ANOVA) with SPSS® Version 15.0 (Apache Software Foundation, Chicago, Illinois). Experimental treatment comprised the among-subjects fixed factor with four and three levels for, respectively, *in*

situ benthos (constant, variable, procedural control and upstream control) and drift (no upstream control treatment). Sampling day provided repeated measures on treatment with five, four and three levels for, respectively, immediate drift, delayed drift and *in-situ* benthos (Fig. 3.2A). Least Significant Difference (LSD) pairwise comparisons with Bonferroni adjustments were used in all analyses to identify significant treatment effects. Before analysis, sphericity of the sample variances for the factor treatment through time were first examined using the test of Mauchly (1940). To account for the strong positive effect of sample size on species richness (*e.g.* Bunge and Fitzpatrick 1993), taxon richness was standardised to the size of the sample with the lowest abundance of invertebrates using rarefaction (Sanders 1968, Hurlbert 1971). Rarefied species richness was then used as the dependent variable in the ANOVA. Owing to the consistently small size of immediate drift samples from the procedural control channels (minimum sample size of two), rarefaction of immediate drift was done only on samples from the disturbed channels. Checks for normality and homogeneity of variance (Levene 1960) were done on all data, and transformations applied when necessary. Reported values for dependent variables are given throughout as mean \pm standard deviation (SD).

I used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001) based on Bray-Curtis (Bray and Curtis 1957) similarity matrices of $\log(x+1)$ -transformed abundance data to examine the effects of varying temporal patterns within perturbations on the compositional and trophic structure of invertebrate drift and benthic assemblages *in situ*. This was done with 9999 permutations of the residuals under the reduced model (Anderson and Ter Braak 2003). Treatment and sampling day comprised the independent variables in these analyses. Similarity percentages analysis (SIMPER; Clarke and Warwick 2001) was used to identify

the contribution of each taxon to pairwise significant differences between treatments. Taxa were considered important if their contribution to percentage dissimilarity was $\geq 3\%$. All multivariate analyses were done with PRIMER[®] (Version 6.1.8; PRIMER-E Ltd., Plymouth, U.K.) with the PERMANOVA+[®] add-in (Version 1.0.1; Anderson and Gorley 2007).

Results

The addition of sediment to the channels successfully produced contrasting patterns of turbidity between the disturbed treatments (Fig. 3.2B). Suspended solid concentrations during sediment pulses were $184.8 \pm 20 \text{ mg L}^{-1}$ for the constant treatment and ranged from 331.1 ± 23.3 to $27.4 \pm 6.9 \text{ mg L}^{-1}$ for the variable treatment. Concentrations of suspended solids in the control channels were $1.1 \pm 0.6 \text{ mg L}^{-1}$. The (log-transformed) dry mass of sediment collected by the sedimentation traps also differed significantly among treatments (ANOVA, $F_{2,8} = 114.67$, $p < 0.001$). Sedimentation rates in the constant and variable disturbance treatments (respectively 32.2 ± 4.7 and $29.2 \pm 6.2 \text{ mg cm}^{-2} \text{ d}^{-1}$) did not, however, differ from each other but were significantly higher than background stream levels ($0.5 \pm 0.2 \text{ mg cm}^{-2} \text{ d}^{-1}$; $p < 0.001$ in both cases).

Disturbance treatment produced no significant differences in algal biomass during the experiment (ANOVA; $F_{3,8} = 1.5$, $p = 0.297$), though at the end of the disturbance regimes (Day 5) both the constant ($0.77 \pm 0.21 \text{ } \mu\text{g chlorophyll } a \text{ cm}^{-2}$) and variable ($0.68 \pm 0.27 \text{ } \mu\text{g cm}^{-2}$) disturbance treatments had considerably lower biomass than both the control ($1.14 \pm 0.25 \text{ } \mu\text{g cm}^{-2}$) and procedural control ($1.05 \pm 0.31 \text{ } \mu\text{g cm}^{-2}$) treatments. The autotrophic index was, however, affected significantly by sediment disturbances ($F_{3,8} =$

21.4, $p < 0.001$). The proportion of autotrophic organic matter in periphyton from disturbed treatments (constant: 251 ± 61 , variable: 234 ± 55) was significantly lower ($p < 0.01$ in both cases) than in undisturbed treatments (procedural control: 144 ± 26 , control: 135 ± 28). Recovery time did not alter significantly any of the periphytic variables (chlorophyll a : $F_{2,16} = 0.1$, $p = 0.887$; AI: $F_{2,16} = 0.8$, $p = 0.472$).

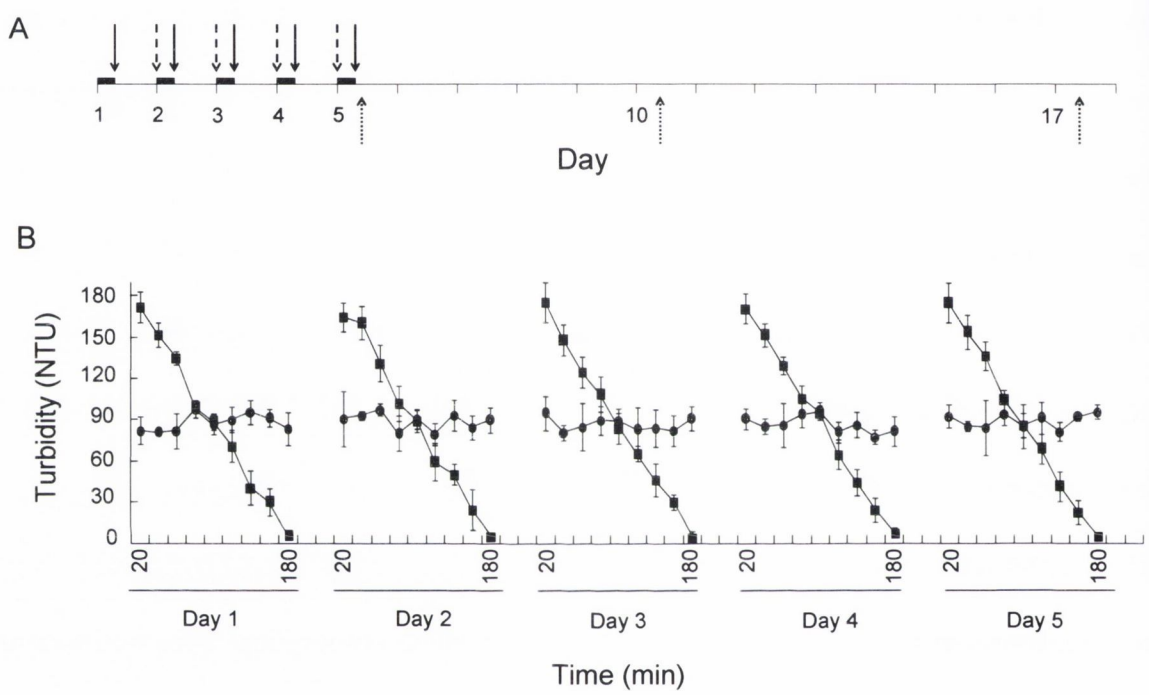


Fig. 3.2. (A) The distribution of sediment perturbations (black rectangles), drift samples (immediate: upper solid arrows, delayed: upper broken arrows) and benthic samples (lower dotted arrows), and (B) resulting mean (\pm SD, $n = 3$) daily turbidities in the constant (closed circle) and variable (closed square) disturbance treatments over the duration of the experiment. Background water turbidity was 0.77 ± 0.30 NTU ($n = 15$).

Invertebrate drift

Thirty eight invertebrate taxa were collected in the drift during the experiment from a total of 45 composing the assemblages found *in situ* (Appendix A). Experimental treatment produced significant differences in the abundance (Table 3.1), assemblage

composition and trophic characteristics (Table 3.2) of invertebrates drifting from the experimental channels during the addition of sediment (immediate drift; Fig. 3.3A). Each treatment differed significantly ($p < 0.001$) from every other for each response variable. The highest immediate drift rates corresponded to the variable treatment and the lowest to the control channels, of which the latter registered very low densities composed almost exclusively of plecopteran shredders. Chironomids, simuliids and a number of plecopteran taxa consistently contributed the most to pairwise differences in the composition of immediate drift between treatments (Table 3.3). No difference was, however, found in rarefied taxon richness of immediate drift between the constant and the variable treatments (Table 1; Fig. 3.3C).

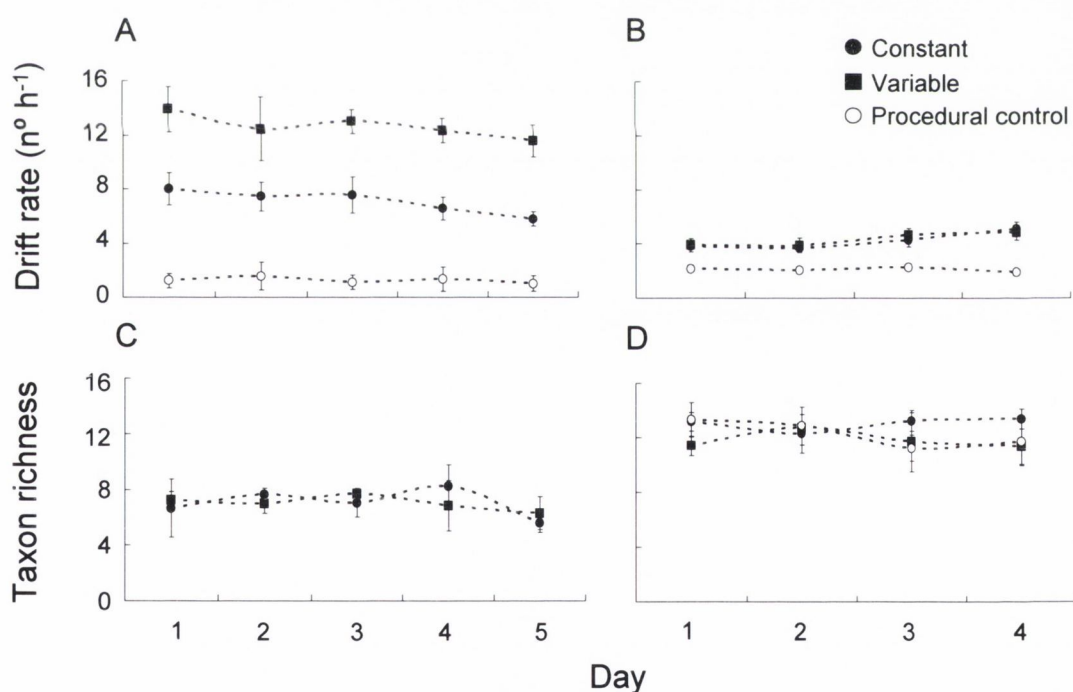


Fig. 3.3. Mean (\pm SD) (A, B) rates and (C, D) rarefied taxon richness of invertebrates drifting from experimental channels during sediment addition (immediate drift; A, C) and during the time elapsed between consecutive pulses (delayed drift; B, D). Results from procedural controls were not included in the calculation of rarefied richness of immediate drift because of low sample size.

Table 3.1. Results of ANOVA examining the effects of sediment disturbance pattern on the abundance and rarefied taxon richness of invertebrate drift and benthic assemblages *in situ*. Statistically significant effects are shown in bold font.

Source of Variation	df	Abundance			Taxon richness		
		MS	F	p	MS	F	p
Immediate drift							
Between subjects							
Treatment	2	4386.8	768.12	<0.001	0.01	0.01	0.949
Error	6	5.7			1.8		
Within subjects							
Day	4	28.8	2.23	0.096	2.5	1.9	0.166
Day x Treatment	8	7	0.55	0.811	1.3	1	0.431
Error	24	12.9			1.3		
Delayed drift							
Between subjects							
Treatment	2	8386.3	47.17	<0.001	4.7	11.6	0.009
Error	6	177.8			0.4		
Within subjects							
Day	3	490.8	15.5	<0.001	0.9	0.46	0.716
Day x Treatment	6	200.2	6.32	0.001	1.9	1.03	0.436
Error	18	31.7			1.9		
Invertebrate benthos in-situ							
Between subjects							
Treatment	3	5127.3	19.3	0.001	35.5	14.4	0.001
Error	8	266.1			2.5		
Within subjects							
Day	2	8804.3	44.7	<0.001	11.9	5.9	0.012
Day x Treatment	6	2758	14	<0.001	0.5	0.25	0.955
Error	16	197.1			2		

Table 3.2. Results of PERMANOVA examining the effects of sediment disturbance pattern on the assemblage composition and trophic structure of invertebrate drift and benthic assemblages *in situ*. Statistically significant effects are shown in bold font.

Source of Variation	df	Assemblage composition			Trophic structure		
		MS	Pseudo-F	p	MS	Pseudo-F	p
Immediate drift							
Treatment	2	16294	16.9	<0.001	19058	59.4	<0.001
Day	4	1123.8	1.2	0.292	156.3	0.5	0.886
Day x Treatment	8	869.2	0.9	0.646	210.6	0.7	0.855
Error	30	963.9			321.1		
Delayed drift							
Treatment	2	2140.1	6.5	<0.001	724.6	16.9	<0.001
Day	3	334.7	1	0.449	76.9	1.8	0.1
Day x Treatment	6	365.7	1.1	0.291	55.1	1.3	0.238
Error	24	329.9			42.9		
Invertebrate benthos							
Treatment	3	1478.7	5.1	0.007	177.8	4.2	0.05
Day	2	752.5	3	<0.001	145.2	18	<0.001
Day x Treatment	6	289.2	1.2	0.185	42.9	5.3	<0.001
Error	24	250.2			8.1		

Experimental treatment and time interacted significantly in their effects on rates of drift occurring between disturbances (delayed drift; Table 3.1). Rates of delayed drift were significantly higher in disturbed (constant and variable) channels than in control channels on every day ($p < 0.001$), with no difference found between the two disturbed treatments (Fig. 3.3B). The number of invertebrates drifting between disturbances from channels under both disturbance treatments increased significantly over the duration of the experiment; delayed drift in both disturbance treatments at the end of the disturbance regime (Day 4) was significantly higher than during the first two days of the experiment ($p < 0.05$). The temporal patterning of sediment disturbances also produced

significant differences in the rarefied taxon richness of delayed drift (Table 3.1; Fig. 3.3D). Richness from the constant disturbance treatment was significantly higher than that from the variable treatment ($p < 0.01$). Delayed drift from neither treatment differed significantly in rarefied taxon richness to that from the procedural controls, however, though the difference between the constant disturbance treatment and the procedural control was bordering on statistical significance ($p = 0.065$).

The taxonomic composition and trophic structure of delayed drift varied significantly among the experimental treatments (Table 3.2). The treatment effect corresponded to a difference between the disturbed and undisturbed treatments ($p < 0.001$), but no difference was found between constant and variable disturbance treatments.

Table 3.3. Principal ($\geq 3\%$) invertebrate taxa contributing (SIMPER) to observed significant differences in assemblage composition of immediate drift and their percentage contribution to the pairwise difference between treatments.

Constant – Variable	%	Variable - Control	%	Constant - Control	%
Simuliidae (D; CF)	11.1	Simuliidae (D; CF)	22.1	Simuliidae (D; CF)	2.3
Chironomidae (D; CG)	9.3	Chironomidae (D; CG)	17.1	Chironomidae (D; CG)	1.8
<i>Chaetopteryx villosa</i> (T; SH)	8.6	<i>L. inermis</i> (P; SH)	9.9	<i>L. inermis</i> (P; SH)	10.1
<i>Siphonoperla torrentium</i> (P; P)	8.1	<i>P. meyeri</i> (P; SH)	8.3	<i>S. torrentium</i> (P; P)	9.5
<i>Protonemura meyeri</i> (P; SH)	6.4	<i>S. torrentium</i> (P; P)	8.3	<i>C. villosa</i> (T; SH)	7.2
<i>Leuctra inermis</i> (P; SH)	6.3	<i>A. sulcicollis</i> (P; SH)	5.9	<i>L. volckmari</i> (C; S)	4.1
<i>Rhyacophila munda</i> (T; P)	6	<i>C. villosa</i> (T; SH)	5.5		
<i>Amphinemura sulcicollis</i> (P; SH)	6	<i>R. munda</i> (T; P)	4		
<i>Rhyacophila dorsalis</i> (T; P)	5.2	<i>R. dorsalis</i> (T; P)	3.3		
<i>Leuctra hippopus</i> (P; SH)	3.6	<i>Limnius volckmari</i> (C; S)	3.2		

Note: D: diptera; T: trichoptera; P: plecoptera; C: coleoptera
SH: shredder; CG: collector-gatherer; CF: collector -filterer; P: predator; S: scraper

The abundance (Table 3.1; Fig. 3.4A) and trophic structure (Table 3.2; Fig. 3.5B) of benthic assemblages *in situ* were both affected significantly by an interaction between treatment and time. Even though abundance in the variable treatment was consistently lower than that in the constant treatment (Fig. 4A), no significant difference was found between the two disturbed treatments. Benthic invertebrate abundance in both disturbed channels (constant and variable treatments) was, however, significantly lower than in the two control treatments both immediately (Day 5) and five days following the last disturbance (Day 10) ($p < 0.05$). Abundances increased significantly ($p < 0.05$) in both the constant and variable disturbance treatments on each sampling day compared with previous days and were similar across all treatments twelve days after the final disturbance (Day 17; Fig. 3.4A).

No difference in trophic structure was found between the variable and constant disturbance treatments over the duration of the experiment. Both, however, differed significantly from the two control treatments on each day ($p < 0.05$) except for 12 days after the final disturbance (Day 17) where the constant treatment remained significantly different from the control treatments ($p < 0.05$) but the variable treatment did not.

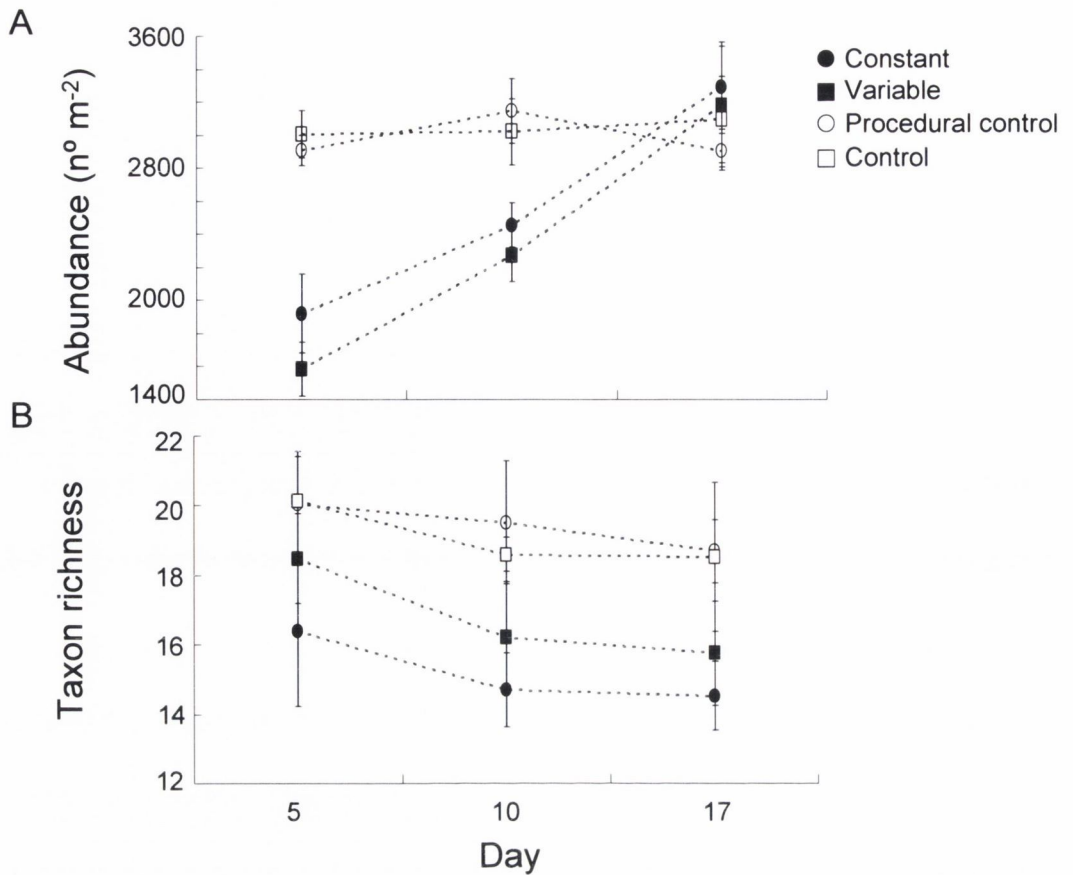


Fig. 3.4. Mean (\pm SD) (A) abundance and (B) rarefied taxon richness of benthic invertebrates *in situ* immediately following cessation of sediment disturbances (Day 5) and during the subsequent recovery period (Day 10, Day 17).

Both the taxon richness (Table 3.1; Fig. 3.4B) and composition (Table 3.2; Fig. 3.5A) of benthic assemblages *in situ* varied significantly with experimental treatment. In both cases, the disturbed treatments (constant and variable) differed significantly ($p < 0.05$) from the two control treatments (controls and procedural controls), which did not differ significantly from each other. No significant differences were, however, found between the two disturbance treatments, even though the taxon richness in the variable treatment was consistently higher than in the constant disturbance treatment for the duration of the experiment (Fig. 3.4B).

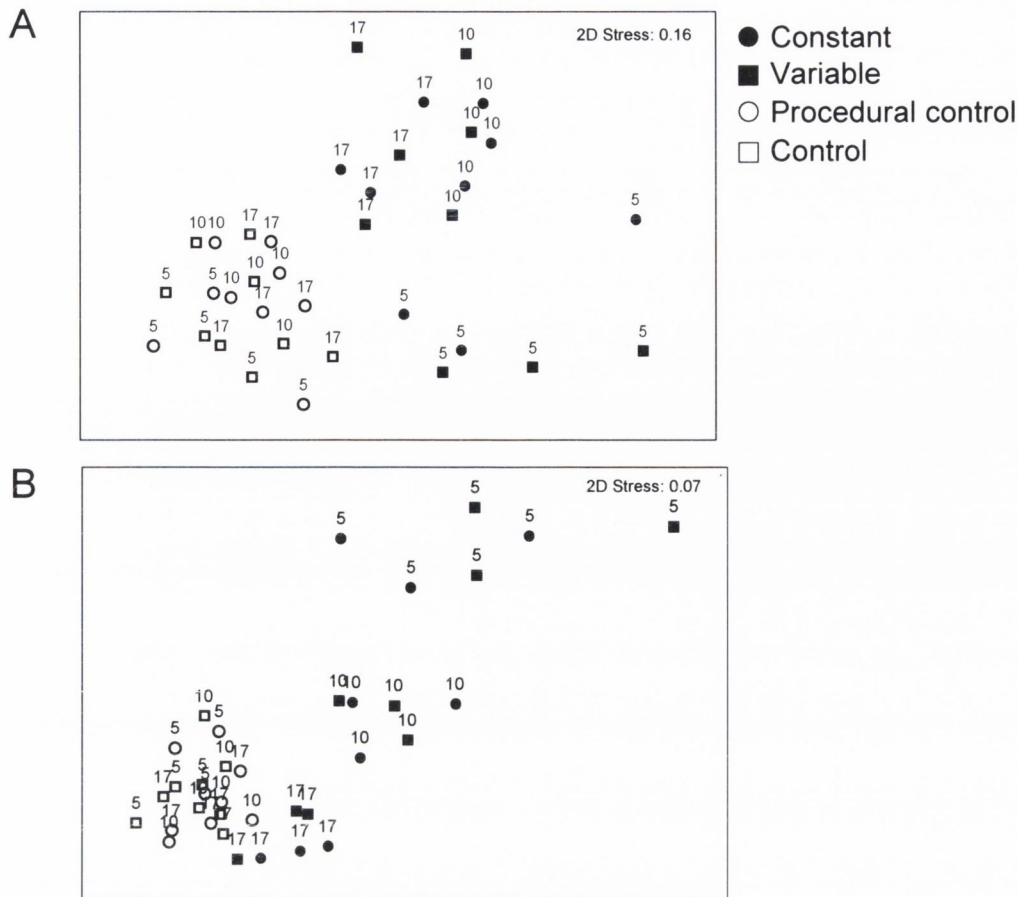


Fig. 3.5. Non-metric multidimensional scaling plots (calculated from Bray-Curtis similarity matrices based on $\log(x+1)$ -transformed abundance data) showing differences in the (A) composition and (B) trophic structure of invertebrate assemblages *in situ* after cessation of disturbances. Numbers by the symbols indicate corresponding sampling day (Day 5 corresponds to the final day of experimental disturbance).

Discussion

My results show clearly that differences in the temporal pattern within individual perturbations can modify the responses of biotic assemblages to disturbances independently of other disturbance attributes. I found significantly differing responses of benthic invertebrate assemblages to the ‘press’ (constant) and ‘ramped’ (variable) pulse disturbances even though the mean intensity, duration, frequency and timing of the perturbations were otherwise identical. These results support the growing body of

literature which indicates the importance of variability around the mean of causal processes as a key determinant of ecosystem patterns (Butler 1989, Menge *et al.* 1994, Navarrete 1996, Sommer 2000, Benedetti-Cecchi *et al.* 2005, Benedetti-Cecchi *et al.* 2006). This study constitutes, however, the first experimental evidence that temporal variability within individual perturbations can drive the responses of biotic assemblages to disturbance independently of other disturbance traits.

Differences in the temporal pattern of sediment pulses regulated the drift patterns of benthic invertebrate assemblages in my experimental channels. Large-scale displacements of invertebrates occur commonly under increased sediment loading (Pearson and Franklin 1968a, Rosenberg and Wiens 1978, Culp *et al.* 1987, Doeg and Milledge 1991, Shaw and Richardson 2001). However, in my experiment, I found remarkably different drift responses between those occurring during disturbances (immediate drift) and those taking place between disturbances (delayed drift). This suggests strongly that the mechanisms behind those responses differed. Further, numbers of invertebrates drifting during temporally variable disturbances were almost double those from the constant perturbations. Moreover, the composition and trophic structure of the invertebrates in the immediate drift also differed between the two disturbed treatments. Temporal variability in the patterning of sediment disturbances appears, therefore, to have been responsible for an enhanced immediate drift response. The greater maxima and higher variability of sediment loading achieved under the variable disturbance treatment may have promoted drift by overriding the tolerance or avoidance capacity of invertebrate taxa to the direct impact of sediment disturbances by physical shear stress (Culp *et al.* 1986, Vuori and Joensuu 1996, Gibbins *et al.* 2007b), increasing physiological impairment owing to clogging of respiratory and feeding body

structures (Lemly 1982, Aldridge et al. 1987, Broekhuizen et al. 2001), or by triggering drift indirectly by, for example, reducing light attenuation (Waters 1995). The fact that the principal taxa contributing to control-disturbance differences in the composition of immediate drift remained largely the same for the two disturbed treatments suggest a higher sensitivity of these taxa to sediment disturbance and seems to indicate that increasing variability exacerbated rather than altered the effect of sediment disturbance on immediate drift.

Between perturbations, no differences were found between the two disturbed treatments in the rates or composition of drift. Rates of delayed drift increased consistently in both disturbed treatments over the duration of the experiment. This was likely a result of the increasing siltation of the stream bed inducing drift by indirect factors such as reduced food quality and availability (Hildebrand 1974, Suren 2005, Peeters et al. 2006) or changes in substrate composition (Ciborowski et al. 1977, García Molinos and Donohue 2009). The mean intensity of the disturbances, rather than their temporal pattern, appears, therefore, to be the main driver of the delayed drift response. I found, however, evidence that rarefied taxon richness of the delayed drift was higher in the constant compared with the variable disturbance treatment. Ecological responses to disturbance are often conditioned by previous stress history (e.g. Knight et al. 1998, Ruane et al. 2002). This result indicates that varying temporal patterns during perturbations may differentially affect invertebrate drift even after disturbances.

Benthic invertebrate assemblages *in situ* did not differ significantly in abundance, diversity or composition between the two disturbed experimental treatments after cessation of all perturbations and over the subsequent recovery period, despite the

strong effect of sediment on all response variables, which is common to this type of disturbance (e.g. Matthaei et al. 2006, Bo et al. 2007, Vasconcelos and Melo 2008, García Molinos and Donohue 2009). However, although not statistically significant, assemblages under the variable treatment registered consistently lower abundance and higher taxon richness over the recovery period. Further, even though benthic assemblages *in situ* under both disturbance treatments experienced some degree of compositional recovery, that occurring in the variable treatment was complete by the end of the experiment, whereas this was not the case in the constant disturbance treatment. Though the mechanisms behind these differences, likely linked to those of the drift, are difficult to establish, their existence indicates that the temporal pattern of sediment disturbances can elicit differential responses of benthic assemblages.

The nature of biological community responses to disturbance-induced changes in resources and environmental conditions comprises a key focus of community ecology (Platt and Connell 2003, Chase 2007, Fraterrigo and Rusak 2008). The development and testing of current theories requires, however, a shift in emphasis from the quantification of resulting ecosystem patterns towards the provision of a mechanistic understanding of the processes that cause and maintain those patterns (Chesson and Huntly 1997, Lake 2000, Roxburgh et al. 2004, Shea et al. 2004). However, it is still common practice in experimental disturbance studies to substitute disturbance intensity by its effects (e.g. percentage of population removal; Speidel 2001, Luttenton and Baisden 2006) or to use a constant value over the duration of a perturbation (e.g. Marshall and Bailey 2004, James et al. 2008). Previous field studies (e.g. Hewitt and Norkko 2007, Crosa et al. 2010) and experiments (e.g. Imbert and Perry 2000, Klironomos et al. 2005) have indicated a differential effect of the temporal pattern of intensity within individual perturbations on

ecosystem responses. However, the effects of the temporal pattern of disturbance in these studies were confounded with those of other disturbance attributes. My experimental design enabled the analysis of the effects of temporal patterns of disturbance independent of other characteristics of disturbances. My results demonstrate that variability in the distribution of disturbance intensity over time can elicit differential biological responses both quantitatively (extent of response) and qualitatively (type of response), even when the overall intensity, duration and frequency of the disturbances are otherwise equal.

My findings have important practical implications. Current environmental management is heavily reliant on the definition of ecological thresholds to establish a point beyond which ecosystem deterioration occurs (Porter et al. 2005, Groffman et al. 2006). These are commonly translated into legislation as the maximum amount of a pollutant that an ecosystem can 'safely' assimilate without deterioration in state or functioning (*e.g.* total maximum daily load in the U.S. Clean Water Act (Public Law 92-500), environmental quality standards in the EU Water Framework Directive (2000/60/EC) and critical loads in the 1979 Geneva UNEC Convention of Long-Range Transboundary Air Pollution). Monitoring programs are then limited usually to the estimation of pollutant loads by comparing monitored acute (*e.g.* daily maximum) or chronic (*e.g.* monthly average) concentrations with the corresponding maximum allowance loads. The use of such absolute values may result in ineffective or inappropriate management decisions by neglecting the existence of any temporal variability in the emission of pollutants (*e.g.* Diamond et al. 2006). This would be particularly the case if, as it has been demonstrated here, the temporal pattern of exposure can affect independently the nature and the extent of ecosystem responses. The mean is a measure of central tendency that can be

reached by several alternative pathways, each possibly with different ecological implications. Similarly, the maximum intensity is an absolute value that does not provide information of the mode in which organisms have been exposed to disturbances. Understanding what mechanisms underlie apparent threshold behaviour is critical for the sensible application of thresholds (Groffman et al. 2006). My results suggest strongly that the quantification of the temporal patterns within as well as among perturbations would advance considerably such understanding.

Chapter IV. Temporal variance mediates effects of compounded perturbations.



General downstream view of experimental site with details of dosing enclosures and colonisation cages (Photo by Jorge García Molinos)

Previous chapters of this thesis have found that both the duration (Chapter II) and the temporal pattern (Chapter III) of individual perturbations can drive biological responses to disturbance. However, human disturbances are frequently a combination of multiple stressors. When multiple agents of disturbance are operating in parallel, the specific temporal pattern of perturbations might be very important in determining ecological responses by influencing the mode of action of individual stressors. Therefore, I investigate here the effects of temporal variability in the definition of compounded sediment and nutrient disturbance effects on stream benthic biota.

Abstract

Recent research has revealed that one of the most important characteristics of both natural and anthropogenic disturbances is their temporal heterogeneity. However, little is known about the relative importance of interactions among temporal patterns of multiple stressors. I established a fully-factorial field experiment to test whether interactions among temporal patterns of two globally important anthropogenic disturbances of aquatic ecosystems (increased sediment loading and nutrient enrichment) determined the responses of stream benthic assemblages. Both disturbance treatments comprised three distinct regimes; regular and temporally variable pulses and an undisturbed control. The overall frequency, intensity and extent of disturbance was, however, equal across all disturbed treatments. I found that interactions among temporal disturbance regimes determined the effects of the compounded sediment and nutrient perturbations on algal biomass and the diversity, taxonomic and trophic composition of benthic assemblages. Moreover, my results also show that the temporal synchronisation of multiple stressors does not necessarily maximize the impact of compounded perturbations. This comprises the first experimental evidence that interactions among the temporal patterns of disturbances drive the responses of ecosystems to multiple stressors. Knowledge of the temporal pattern of disturbances is therefore essential for the reliable prediction of impacts from, and effective management of, compounded perturbations.

Introduction

The increasing global human domination of ecosystems (Vitousek *et al.* 1997) is threatening the ecological integrity of the entire biosphere (Chapin *et al.* 2000, Thomas *et al.* 2004). There is, therefore, a critical need for effective management to minimize the effects of human disturbance on ecosystems. Key to this is the ability to understand and predict the effects of disturbance on fundamental ecosystem processes. In particular, quantification of interactions among multiple stressors comprises one of the most pressing problems in ecology and conservation (Breitburg *et al.* 1998, Wilcove *et al.* 1998, Sala *et al.* 2000, Rhind 2009). The coupling of multiple stressors can produce complex and unforeseen interactive effects on ecosystems (Heugens *et al.* 2002, Sih *et al.* 2004, Vinebrooke *et al.* 2004). Moreover, the nature of such interactions may themselves change after the introduction of additional stressors (Crain *et al.* 2008). These findings demonstrate a clear and urgent need for increased understanding of the mechanisms underlying the interactive effects of multiple stressors on ecosystems.

Studies of the effects of disturbance on ecosystem processes have focused mostly on the mean effect of properties such as the intensity, extent or frequency of perturbations (*e.g.* McCabe and Gotelli 2000, Collins *et al.* 2001). However, theoretical (Benedetti-Cecchi 2003), experimental (Benedetti-Cecchi *et al.* 2005, Bertocci *et al.* 2005) and observational (Underwood and Chapman 2000) studies demonstrate that variability around the process mean, or variability in the distribution of disturbance events over time or in space, can comprise a key driver of ecosystem responses to disturbance. Recent field experiments have, for example, shown that variation in the temporal pattern of disturbance both among (Benedetti-Cecchi *et al.* 2006) and within (Chapter III

in this thesis) individual perturbation events can determine the overall effects of disturbances, even when the frequency, extent and mean intensity of the disturbances remain constant. Moreover, such high temporal variability is common to most types of both natural and human disturbances (*e.g.* Ferrier *et al.* 2001, Villarini *et al.* 2009). Quantification of the effects of interactions among variable temporal patterns on ecosystems where multiple agents of disturbance are acting in parallel comprises, therefore, an important step towards improving our understanding of the mechanisms underlying the interactive effects of multiple stressors.

I designed a fully-factorial field experiment to quantify the interactive effects among variable temporal patterns of a compounded disturbance regime comprising two of the most globally important and widespread human stressors on aquatic ecosystems; increased loading of sediments (Waters 1995, Donohue and García Molinos 2009) and nutrients (Carpenter *et al.* 1998, Donohue *et al.* 2009, Smith and Schindler 2009), on the biota of a headwater stream. Compounded sediment-nutrient perturbations are common in aquatic ecosystems because they are linked to a large and diverse list of anthropogenic activities and often share the same sources (Allan 2004, Wohl 2006, Banas *et al.* 2008). I assessed the individual and combined effects of these two stressors under three distinct temporal regimes (regular and temporally variable pulses and an undisturbed treatment) on both periphyton and benthic invertebrate assemblages. The overall frequency, intensity, duration and extent of the disturbances were, however, equal across all disturbed treatments. The aim of this work was to test the hypothesis that the effects of multiple stressors on ecosystem processes depend upon the interaction between their respective temporal patterns.

Methods

Experimental design

The experimental site comprised a pristine uniform riffle reach of a fourth order stream (Glencree River, County Wicklow, Ireland; 53°10.23' N, 06°12.18' W). The site was 16 m wide, fringed by riparian vegetation and had uniform bed morphology throughout, dominated by material in the cobble-pebble range. The mean (\pm SD) water depth at the site for the duration of the experiment (May 2009) was 11 ± 3 cm ($n = 376$).

This fully-factorial experiment comprised two treatments; temporal patterns of sediment and nutrient disturbances, both fixed factors with three levels each (undisturbed, a regular disturbance regime and a temporally variable disturbance regime). There were four replicates per treatment. Disturbance frequency for all disturbed treatments totalled ten perturbations over the duration of the experiment (30 days). Whereas the regular disturbance regime had a disturbance frequency of one perturbation every three days, the temporally variable regime maximized the temporal variability of perturbations (*i.e.* maximized the standard deviation of the mean interval length between perturbations; Fig. 4.1). However, to ensure that both the length of disturbance and time for recovery after disturbance was equal across all disturbed treatments, the first and the last perturbations across all disturbed treatments took place on the same day (Fig. 4.1).

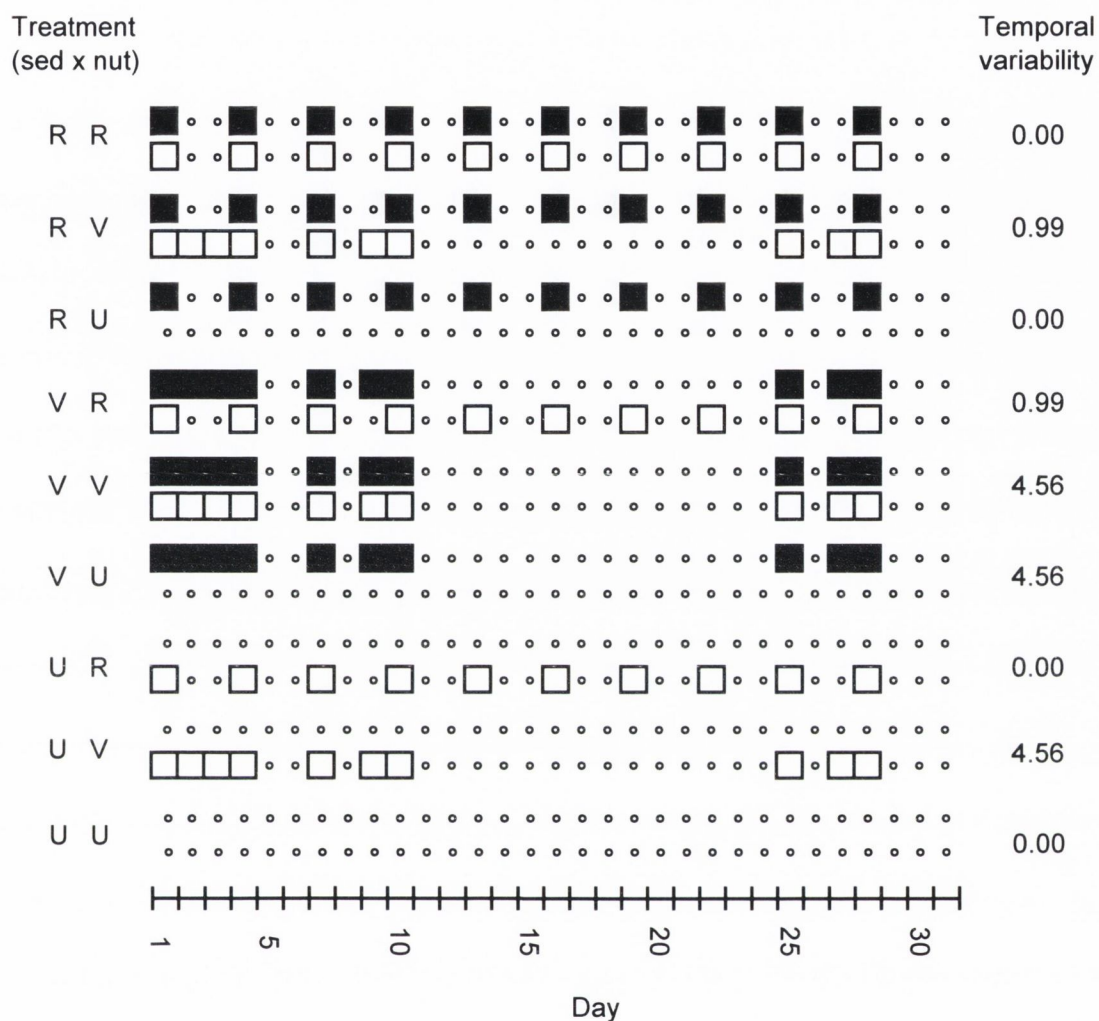


Fig. 4.1. Schematic representation of experimental treatments resulting from a 3x3 full-factorial design crossing temporal patterns of sediment (filled squares) and nutrient (open squares) disturbance regimes with three levels each: regular (R), variable (V) and undisturbed (U). Temporal variability is expressed as the standard deviation of the mean interval length (in days) between perturbations.

I used open-topped polyvinyl chloride (PVC) cages (25 cm diameter x 10 cm high) filled with substratum taken 10 m downstream of the experimental site as artificial colonisation plots for each experimental unit. The cages were perforated with 1 cm holes every 4 cm arranged in alternating rows and were embedded with 15 cm spacing between each cage in a transect across the experimental site (*i.e.* perpendicular to the direction of flow) six weeks prior to the commencement of the experiment. Experimental treatments were assigned randomly to plots. Three brush-cleaned cobbles of similar size and texture were placed on the top of each plot for quantification of periphyton biomass at the end of the experiment. Plots on either end of the transect were approximately 1 m from the stream bank. I disturbed the plots experimentally by dosing them with sediments and/or nutrients through a PVC pipe of 0.5 m length and of slightly greater diameter to that of the cages (0.3 m) which was fixed carefully to the stream bed to create an enclosure which isolated the plot from its neighbors. Sediment perturbations consisted of the addition of 1 kg of sieved (<2 mm) gardening soil which was spread evenly over the entire surface of the enclosure. The soil comprised 41% very coarse sand (1-2 mm), 30% coarse sand (0.5-1 mm), 14% medium sand (250-500 μm), 7% fine sand (125-250 μm), 5% very fine sand (63-125 μm), and 3% silt and clay (<63 μm). Nutrient perturbations were done by adding concentrated (1 g L⁻¹) sodium hydrogen orthophosphate and ammonium nitrate solutions to the enclosures to increase concentrations of P and N to 200 $\mu\text{g L}^{-1}$ above ambient levels. Both sediment and nutrients were added simultaneously where necessary (Fig. 4.1). After perturbation, dosing enclosures were left in place for one hour. To ensure procedural consistency, enclosures were also placed on the undisturbed treatments. The removal of enclosures from plots perturbed with sediment generally resulted in most of the deposited sediments being washed downstream. Measurements taken during the experiment

showed, however, that both sediment and nutrient perturbations were operating as intended (see Results).

To examine the effectiveness of the nutrient perturbations, I took weekly water samples randomly from three of the enclosures receiving nutrient enrichment and one of the undisturbed plots for quantification of both reactive soluble phosphorus (RSP) and dissolved inorganic nitrogen (DIN) for the duration of the experiment. DIN was quantified by flow injection analysis (Lachat QuickChem® 8500; Lachat Instruments, Milwaukee, USA) following standard methods (Clesceri *et al.* 1999) while RSP was quantified spectrophotometrically following Murphy and Riley (1962). I examined the effectiveness of the sediment perturbations by estimating visually fine sediment (<2mm) cover at the end of the experiment as the % cover of each plot, in 5% increments, covered by fine material (Zweig and Rabeni 2001).

I collected all experimental plots 30 days after the initial perturbation. Cobbles for quantification of periphyton biomass were removed carefully prior to extraction of the cages from the stream bed. Sampling and analysis of periphyton followed procedures described in previous chapters of this thesis (Chapter II and III). Chlorophyll *a* concentration and the autotrophic index were used respectively as indicators of periphytic biomass and its relative viability. The experimental plots were then removed from the stream bed and preserved immediately on site with ethanol. Invertebrates in the plots were sorted and identified to the lowest taxonomic level practicable in the laboratory. Each taxon was also assigned to a functional feeding group following Merritt and Cummings (1996).

Statistical analysis

Effects of experimental treatments on univariate biotic variables were tested with analysis of variance (ANOVA). Dependent variables were log-transformed where necessary to meet assumptions of normality and homoscedasticity. I used both rarefied taxon richness, and Shannon's index of diversity (H' ; calculated using \log_e) as measures of invertebrate diversity. Rarefied taxon richness was used to unconfound the effect of abundance on taxon richness by standardizing to the sample with the lowest abundance (Hurlbert 1971). Where significant treatment effects were found, Student Newman-Keuls (SNK) post hoc procedures (Underwood 1997) were used to test for differences among treatment levels. Statistical analyses were done with SPSS® Version 15.0 (Apache Software Foundation, Chicago, Illinois).

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001) was used to test for treatment effects on both the taxonomic and trophic composition of benthic invertebrate assemblages. These analyses were based on Bray-Curtis similarity matrices calculated from $\log(x+1)$ -transformed abundance data with 9999 permutations of the residuals under the reduced model and were done with PRIMER® Version 6.1.8 (PRIMER-E Ltd., Plymouth, U.K.) and the PERMANOVA+® add-in (Version 1.0.1). I also applied the Newman-Keuls procedure (Underwood 1997) to the pairwise PERMANOVA post hoc tests. Results for dependent variables are reported throughout as mean \pm standard deviation (SD). An α significance level of 0.05 was used for all analyses.

Results

Concentrations of RSP in the nutrient enriched plots (mean \pm SD: $190 \pm 18 \mu\text{g L}^{-1}$; $n = 12$) were over 30 times greater than those in the undisturbed treatments ($6 \pm 1 \mu\text{g L}^{-1}$; $n = 4$), while those of DIN were almost doubled (nutrient enriched treatments: $472 \pm 31 \mu\text{g L}^{-1}$; undisturbed treatments: $261 \pm 21 \mu\text{g L}^{-1}$). Fine sediment cover of experimental cages increased significantly as a consequence of sediment addition (ANOVA; $F_{2,35} = 130.9$; $p < 0.001$). Cover of fine material in cages under sediment disturbance (regular disturbance regime: $71 \pm 8\%$; variable disturbance regime: $66 \pm 6\%$) was significantly higher ($p < 0.001$) than that in cages with no experimental sediment perturbation ($32 \pm 6\%$). No difference in fine sediment cover was, however, found between the regular and temporally variable sediment disturbance regimes.

Periphyton chlorophyll *a* was affected significantly by the interaction between the temporal patterns of sediment and nutrient disturbances (Table 4.1, Fig. 4.2A). *Post hoc* tests (Table 4.2(A)) found that, within each nutrient disturbance regime, periphyton chlorophyll *a* concentrations were lowest in the regular sediment disturbance regime, followed by those in the variable sediment disturbance regime which were, in turn, lower than those in the treatment undisturbed by sediments. However, nutrient addition only had an effect within the variable sediment disturbance regime, where periphytic chlorophyll *a* was significantly higher in the regular nutrient regime than in both the variable regime and the treatment undisturbed by nutrients. No significant interaction among treatments was found on the ratio of total to autotrophic organic material in periphytic samples, however, which was only affected significantly by the addition of sediment (Table 4.1, Fig. 4.2B). The autotrophic index under the regular

sediment disturbance regime was significantly higher than both the variable and undisturbed sediment regimes ($p < 0.05$), which did not differ significantly from each other.

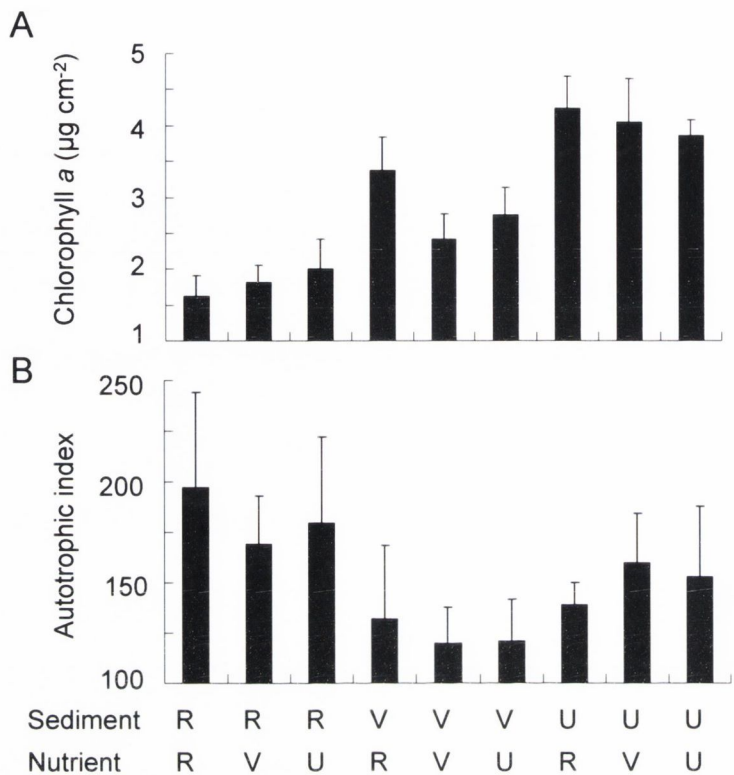


Fig. 4.2. Mean (\pm SD) (A) concentrations of periphytic chlorophyll *a* and (B) autotrophic index in each experimental disturbance regimes ($n = 4$). R: regular disturbance regime, V: variable disturbance regime, U: undisturbed.

A total of 46 invertebrate taxa was recorded from the experimental samples (Appendix B). Significant interactions were found between the temporal patterns of sediment and nutrient disturbances on the Shannon diversity of benthic invertebrates (Table 4.1, Fig. 4.3C). The interaction among treatments was also bordering on significance for rarefied taxon richness ($p = 0.06$; Fig. 4.3B). Results of *post hoc* comparisons for the (Shannon) diversity of benthic invertebrates (Table 4.2(B)) were similar to those of periphytic chlorophyll *a*, with the exception of no sediment effect within the variable nutrient regime, which itself had however significant lower diversity than in both other nutrient treatments in the absence of a sediment disturbance.

Table 4.1. Results of ANOVA examining the effects of experimental treatments on periphyton and benthic invertebrates. Autotrophic index and invertebrate abundance were log-transformed prior to analysis. Statistically significant effects are shown in bold font.

Variable	Treatment	df	MS	F	p
Periphyton					
<i>Chlorophyll a</i>					
	Sediment temporal pattern, S	2	15	94.7	<0.001
	Nutrient temporal pattern, N	2	0.31	1.9	0.165
	S*N	4	0.45	2.9	0.042
	Residual	27	0.16		
<i>Autotrophic index</i>					
	S	2	0.08	11.1	<0.001
	N	2	0.001	0.1	0.924
	S*N	4	0.004	0.6	0.698
	Residual	27			
Benthic invertebrates					
<i>Abundance</i>					
	S	2	0.82	120.57	<0.001
	N	2	0.01	1.74	0.19
	S*N	4	0.01	1.54	0.22
	Residual	27	0.007		
<i>Rarefied taxon richness</i>					
	S	2	55.82	26.8	<0.001
	N	2	5.18	2.5	0.1
	S*N	4	5.33	2.6	0.061
	Residual	27	2.08		
<i>Shannon diversity</i>					
	S	2	0.19	44.3	<0.001
	N	2	0.05	12.19	<0.001
	S*N	4	0.02	4.09	0.01
	Residual	27	0.004		

Table 4.2. Results of SNK *post hoc* tests elucidating the interactions between sediment and nutrient disturbance regimes on (A) periphyton chlorophyll *a*, (B) benthic invertebrate diversity (Shannon’s index) and the (C) taxonomic and (D) trophic composition of benthic invertebrate assemblages. R: regular disturbance regime; V: variable disturbance regime, U: undisturbed.

	Within variable	Level	Comparison
(A)	Nutrient regime	R	Sediment R <(**) Sediment V <(**) Sediment U
		V	Sediment R <(*) Sediment V <(**) Sediment U
		U	Sediment R <(*) Sediment V <(**) Sediment U
	Sediment regime	R	Nutrient R = Nutrient V = Nutrient U
		V	Nutrient R >(*) Nutrient V = Nutrient U
		U	Nutrient R = Nutrient V = Nutrient U
		R	Sediment R = Sediment V = Sediment U
		V	Nutrient R >(**) Nutrient V = Nutrient U
		U	Nutrient R >(**) Nutrient V <(*) Nutrient U
(B)	Nutrient regime	R	Sediment R <(**) Sediment V = Sediment U
		V	Sediment R = Sediment V = Sediment U
		U	Sediment R <(**) Sediment V <(**) Sediment U
	Sediment regime	R	Nutrient R = Nutrient V = Nutrient U
		V	Nutrient R >(**) Nutrient V = Nutrient U
		U	Nutrient R >(**) Nutrient V <(*) Nutrient U
		R	Sediment R = Sediment V = Sediment U
		V	Nutrient R >(**) Nutrient V = Nutrient U
		U	Nutrient R >(**) Nutrient V <(*) Nutrient U
(C)	Nutrient regime	R	Sediment R ≠(*) Sediment V ≠(*) Sediment U
		V	Sediment R = Sediment V ≠(*) Sediment U
		U	Sediment R ≠(*) Sediment V ≠(*) Sediment U
	Sediment regime	R	Nutrient R = Nutrient V = Nutrient U
		V	Nutrient R = Nutrient V = Nutrient U
		U	Nutrient R = Nutrient V = Nutrient U
		R	Sediment R = Sediment V = Sediment U
		V	Nutrient R = Nutrient V = Nutrient U
		U	Nutrient R = Nutrient V = Nutrient U
(D)	Nutrient regime	R	Sediment R ≠(*) Sediment V ≠(*) Sediment U
		V	Sediment R ≠(*) Sediment V ≠(*) Sediment U
		U	Sediment R ≠(*) Sediment V ≠(*) Sediment U
	Sediment regime	R	Nutrient R = Nutrient V = Nutrient U
		V	Nutrient R ≠(*) Nutrient V = Nutrient U
		U	Nutrient R = Nutrient V = Nutrient U
		R	Sediment R = Sediment V = Sediment U
		V	Nutrient R = Nutrient V = Nutrient U
		U	Nutrient R = Nutrient V = Nutrient U

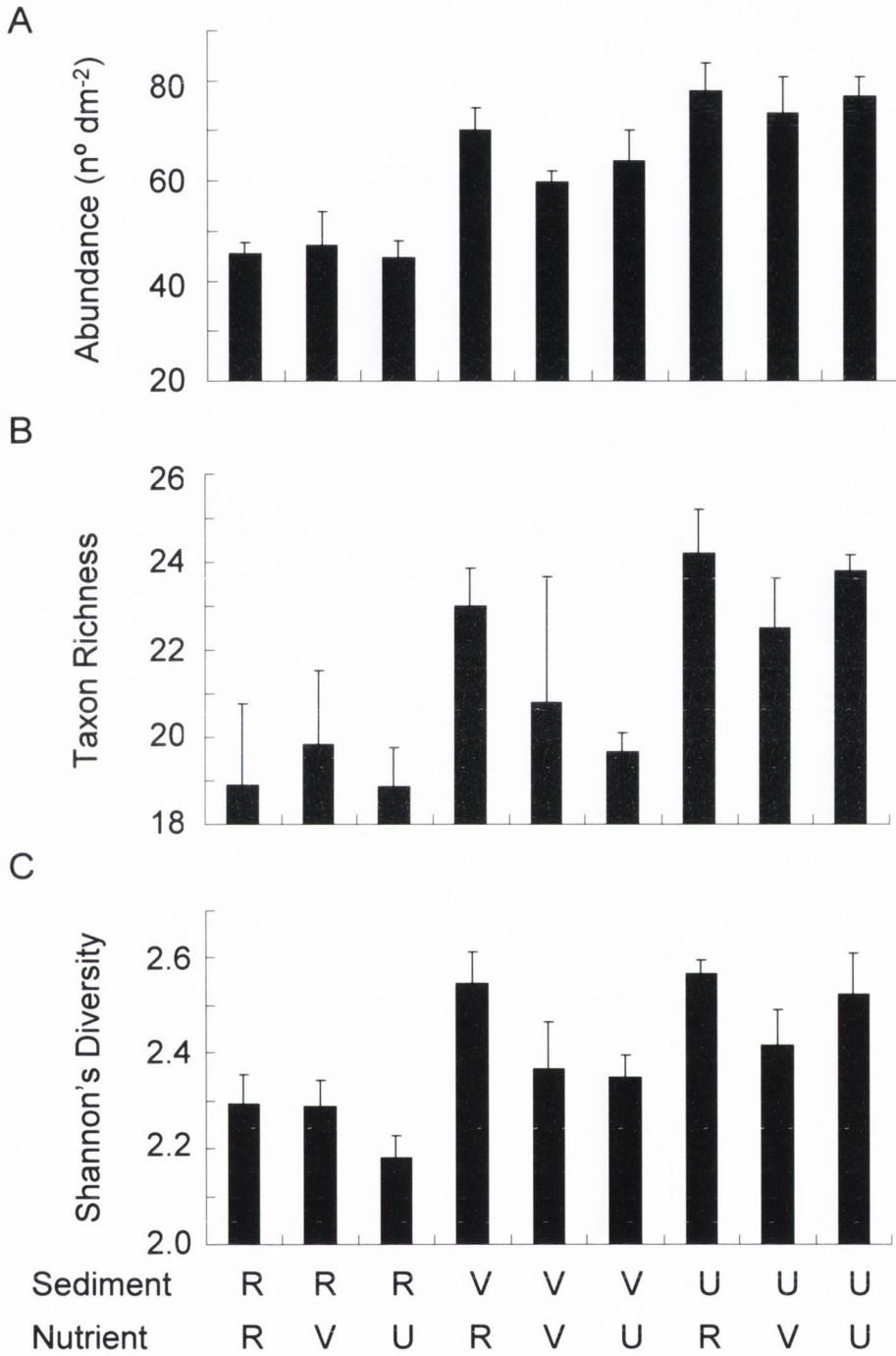


Fig. 4.3. Mean (\pm SD) (A) invertebrate abundance, (B) rarefied taxon richness and (C) Shannon's diversity of benthic invertebrates in each experimental disturbance regime ($n = 4$). R: regular disturbance regime, V: variable disturbance regime, U: undisturbed.

For the invertebrate variables that were not affected significantly by the interaction between experimental treatments (*i.e.* the abundance and rarefied taxon richness of benthic invertebrates; Table 4.1, Figs. 4.3A, B), no effect of nutrient enrichment was found in either case whereas the effects of sediment addition were consistently most negative in the regular disturbance regime and were also significantly lower in the variable regime compared with the treatments undisturbed by sediments ($p < 0.01$ in each case).

The interaction between the sediment and nutrient disturbance regimes affected significantly both the taxonomic and trophic composition of benthic invertebrate assemblages (Table 4.3). Within each nutrient regime, every sediment disturbance regime almost always differed significantly from every other in both taxonomic and trophic composition (Table 4.2(C), (D)). Sediment disturbances resulted in a general decline in the relative abundances of scraper, collector filterer and predator guilds, while the proportions of generalist collector gatherers increased drastically, particularly under the regular disturbance regime (Figs. 4.4 and 4.5). No conclusive effect of nutrient regime on taxonomic composition was, however, found within any of the sediment disturbance regimes (Table 4.2(C)), whereas the regular nutrient regime differed significantly in trophic composition from both the variable nutrient regime and the treatment undisturbed by nutrients when the frequency of sediment disturbances varied over time (Table 4.2(D)). This likely reflects an increase in the proportion of scrapers and a decrease of predators and collector filterers in the variable sediment and regular nutrient treatment (Figs. 4.4 and 4.5).

Table 4.3. Results of PERMANOVA examining the effects of experimental treatment on the taxonomic and trophic composition of benthic invertebrate assemblages. Statistically significant effects are shown in bold font.

Variable	Treatment	df	MS	Pseudo-F	<i>p</i>
Taxonomic composition	Sediment temporal pattern, S	2	1594.6	9.65	<0.001
	Nutrient temporal pattern, N	2	182.1	1.11	0.33
	S*N	4	229.6	1.4	0.034
	Residual	27	164.2		
Trophic composition	S	2	207.7	31.37	<0.001
	N	2	10	1.51	0.2
	S*N	4	17.1	2.58	0.011
	Residual	27	6.6		

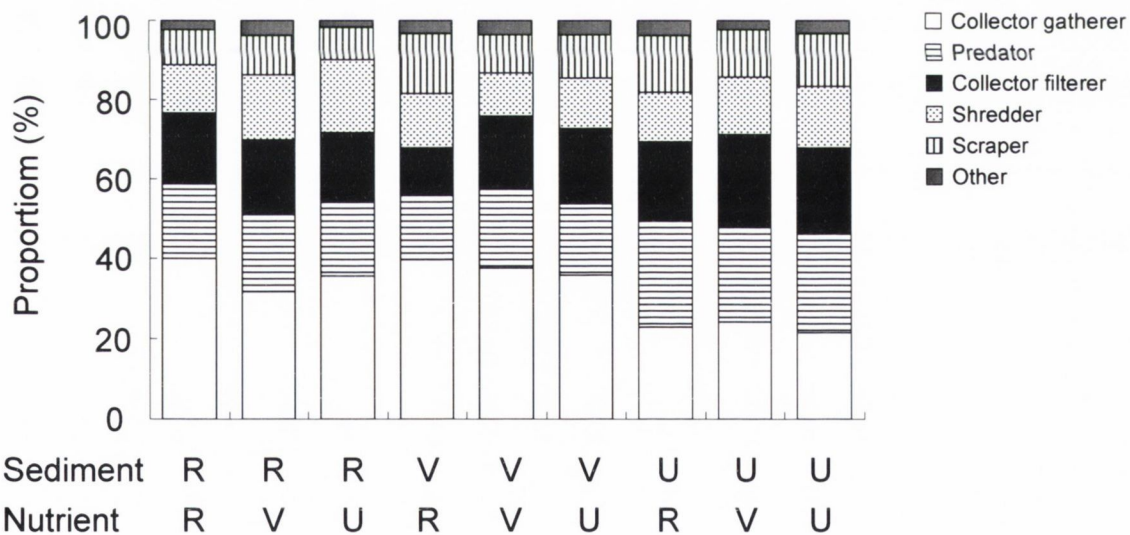


Fig. 4.4. Proportions of functional feeding groups in invertebrate assemblages in each experimental treatment. R: regular disturbance regime, V: variable disturbance regime, U: undisturbed.

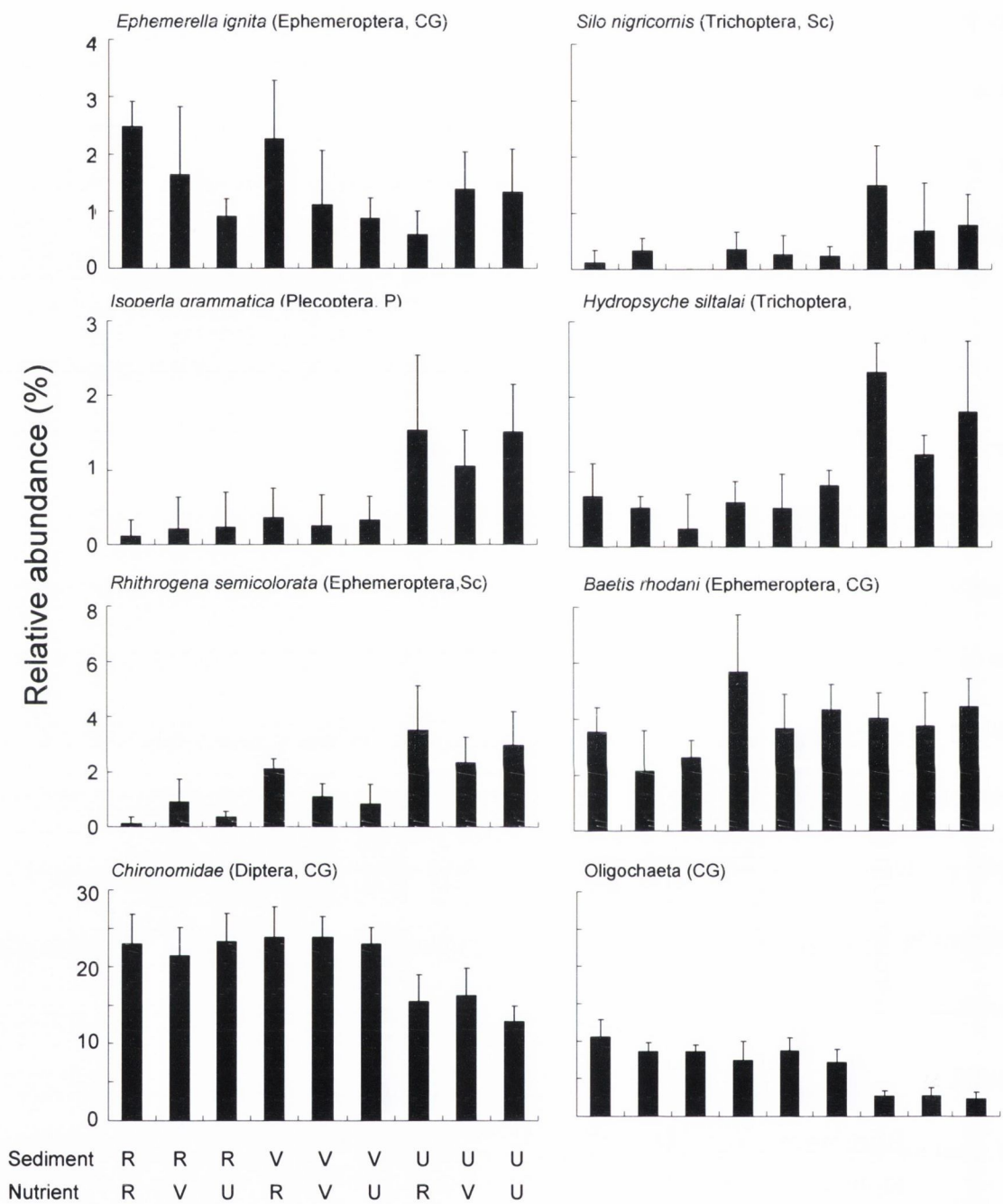


Fig. 4.5. Mean (\pm SD) relative abundance of selected benthic invertebrate taxa in each experimental treatment ($n = 4$). CG: collector-gatherer, CF: collector-filterer, P: predator; S: scraper. R: regular disturbance regime, V: variable disturbance regime, U: undisturbed.

Discussion

My results demonstrate clearly that interactions among the temporal patterns of multiple stressors determine the responses of ecosystems to disturbances. I found significant interactions between the temporal patterns of sediment and nutrient disturbances on each of periphyton biomass and the diversity, taxonomic and trophic composition of stream benthic invertebrate assemblages. These patterns occurred in spite of the fact that the overall frequency, intensity and extent of the disturbances were equal across all disturbed treatments. This study therefore provides the first empirical evidence evincing a key role of interactions among temporal patterns of disturbance in driving the effects of multiple stressors on biotic assemblages. Nutrient enrichment frequently had no effect on stream biota except when delivered in regular pulses in combination with temporally variable sediment perturbations. This highlights the ecological importance of compounded perturbations even when their constituent stressors produce little or no effect individually. Moreover, these interactions were driven by the combined action of asynchronous disturbances (*i.e.* regular sediment and temporally variable nutrient regimes), which indicates strongly that the temporal synchronization of multiple stressors does not necessarily maximise the responses of biotic assemblages to compounded perturbations.

Ecological responses to multiple stressors result from the specific interaction between the characteristics of the disturbed system and the nature and mode of action of the stressors (Breitburg *et al.* 1998). As in other studies (Coker 1987, Coker *et al.* 1990, Townsend *et al.* 2008), I found that sediment and nutrients elicited a general pattern of opposing effects on benthic biota; a normal situation given their very different modes of

action. Overall, the effects of sediment addition on response variables overrode those produced by nutrient enrichment. Nutrient enrichment had no discernable effect on any of the biotic response variables in my experiment in treatments undisturbed by sediments. This was in spite of the fact that concentrations of nutrients, particularly phosphorus, the primary driver of eutrophication in aquatic ecosystems (Schindler *et al.* 2008), were increased dramatically above ambient levels. Moreover, the experiment took place at the height of the growing season and the experimental site was shallow and under good light conditions. Previous studies (*e.g.* Scinto and Reddy 2003, McCormick *et al.* 2006) have shown that periphyton affinity for phosphorus is often translated into high uptake rates in response to similar short-term nutrient pulses. The reasons for the lack of an effect of nutrients in my experiment in the absence of sediment disturbances are, therefore, unclear but may be related to the lower specificity of sediment disturbances (which mechanism of action impacts directly both primary producers and consumers) and their more persistent effect (via deposited material) as compared to the more ephemeral nutrient disturbances whose effects were more limited to the duration of dosage.

That nutrient addition had no effect on biotic assemblages except in combination with the temporally variable sediment disturbance regime suggests that the addition of sediments in some way facilitated ecological responses to nutrient enrichment. Instant algal biomass reductions under the addition of sediment were likely a consequence of increased shear stress produced by deposited particles being washed away from exposed stone surfaces following removal of dosing enclosures (*e.g.* Biggs and Thomsen 1995, Francoeur and Biggs 2006). However, this mechanism of biomass loss may also offer an explanation for the relative higher algal biomass observed under the variable

sediment regime with regular nutrient enrichment. This effect may be a consequence of the scouring effect of the clustered perturbations in this sediment disturbance regime exposing a thin film of productive algal cells to better light conditions and increased access to water column nutrients during the relatively long undisturbed period (McCormick and Stevenson 1991, Azim and Asaeda 2005). Such removal of overstory biomass frequently results in increased productivity and rapid growth of benthic algae (*e.g.* Fisher *et al.* 1982, Lamberti *et al.* 1989, Peterson and Stevenson 1992, Wellnitz and Poff 2006), which would, therefore, be expected to have knock-on effects on upper trophic levels. Regular nutrient enrichment likely intensified this effect resulting in the significant interactions detected in the experiment. A complementary indirect buffering mechanism of nutrient enrichment in the sediment-water interface may have subsidised direct uptake from the water column contributing to enhanced periphytic regrowth. Such mechanism would involve P uptake onto deposited fine-grained sediment and subsequent gradual release during periods of low ambient P concentrations (Froelich 1988, Haggard *et al.* 2005).

Sediment disturbance *per se* reduced both the abundance and diversity of benthic assemblages, with regular pulses of sediments eliciting stronger biotic responses than temporally variable ones. Whereas the regular sediment perturbations were equally spaced over time and without a defined undisturbed period, the clustering of sediment disturbances under the variable regime likely facilitated biotic recovery during the subsequent prolonged undisturbed period. The patch-scale of the experiment, which provided a large and abundant pool of potential colonisers from surrounding undisturbed areas, together with the high resilience that is characteristic of stream ecosystems, probably facilitated this process (Williams and Hynes 1976, Lake 2000).

Whereas the rapid succession of sediment perturbations under the variable regime likely produced a drastic reduction in abundance of most organisms, initial resource limitation and habitat homogenisation may have conditioned the recovery process, favouring species with generalist and/or opportunistic traits against more specialist taxa (Airoldi *et al.* 2008). Regular nutrient disturbances, however, seem to have compensated to some extent these effects favouring the formation of a comparatively more abundant and diverse assemblage. Biological factors such as the identity of post-disturbance remnant species (Platt and Connell 2003, Ledger *et al.* 2006) and the order of species arrival during colonisation (Robinson and Edgemon 1988, Price 2004) may also have influenced post-disturbance recovery, contributing to the observed assemblage differences among treatments. The decline in abundance of large predators and territorial caddis flies in the variable sediment and constant nutrient treatment could, for example, have influenced the observed relative increase of actively swimming baetid mayflies attracted by a comparatively more accessible and abundant periphyton (Scrimgeour *et al.* 1994).

In conclusion, previous studies have shown that temporal variability of single-stressor disturbance regimes comprises an important driver of disturbance-driven biological responses (Bertocci *et al.* 2005, Benedetti-Cecchi *et al.* 2006, Bertocci *et al.* 2007). My results demonstrate that such variability can also determine the effects of compounded disturbances on ecosystems by regulating the mode of action of their constituent stressors. Moreover, my results highlight the fact that interactions among the temporal patterns of multiple stressors can affect biotic assemblages significantly even when their constituent stressors produce little or no effect individually. Further, this study demonstrates that the temporal synchronization of distinct disturbances does not necessarily maximize the impact of compounded perturbations. With few exceptions

(e.g. Fukami 2001) manipulative tests on the effects of multiple stressors are based on non-variable synchronised disturbances (e.g. Folt *et al.* 1999, Relyea and Mills 2001, Coors and Meester 2008). These findings therefore demonstrate that knowledge of the temporal patterns of disturbances is essential for the reliable prediction of impacts from, and effective management of, multiple stressors. The alteration of natural disturbance regimes at both local (Allan 2004) and global (Christensen and Christensen 2003) scales, even in the absence of changes in disturbance intensity *per se*, may, therefore, have dramatic and unforeseen consequences for the integrity of ecosystems globally.

Chapter V. General discussion



River Liffey at Kippure State (Photo by Jorge García Molinos)

This chapter synthesises the results of the preceding chapters and discusses how they address the main hypothesis of this thesis, that sediment disturbance effects on benthic assemblages are regulated by varying temporal disturbance attributes independently of other disturbance traits.

Direct human perturbations and the rapid alteration of natural disturbance regimes owing to land use and climate global change are major challenges for environmental management and conservation (Sala *et al.* 2000, Tilman and Lehman 2001, Foley *et al.* 2005) and comprise one of the biggest problems currently facing humankind (Chapin *et al.* 2000, Smail 2002, Foley *et al.* 2005). Predicted scenarios of future human environmental change suggest a tendency towards increased temporal variability of disturbance regimes (*e.g.* Muller and Stone 2001, Christensen and Christensen 2003, Syphard *et al.* 2009). It is not yet clear, however, how these changes will determine the effects of disturbance on ecosystem processes. This thesis explores the importance of the temporal properties of disturbance for driving ecosystem responses and examines the mechanisms that mediate those effects.

The effect of disturbances on biological systems can be seen as a trade off between their capacity to withstand the damaging force and their ability to make use of the new scenario created by the disturbance (*i.e.* changes in resources, the physical environment and biological interactions) (Sousa 1984, Pickett and White 1985, Chase and Leibold 2003, Shea *et al.* 2004). Immediate direct disturbance effects (*e.g.* mortality) are thus often replaced by subsequent indirect effects mediated via disturbance-induced changes in abiotic and biotic conditions (*e.g.* Effenberger *et al.* 2006, Effenberger 2008). The main hypothesis of this thesis addresses this general pattern of effects from the perspective of the temporal dimension of disturbances. Theory suggests that factors such as the duration and temporal patterning of the disturbing forces should mediate the effects of disturbance regimes independently of other disturbance traits. The results from my manipulative experiments suggest a conceptual model of the effects of these temporal properties that supports this hypothesis (Fig. 5.1).

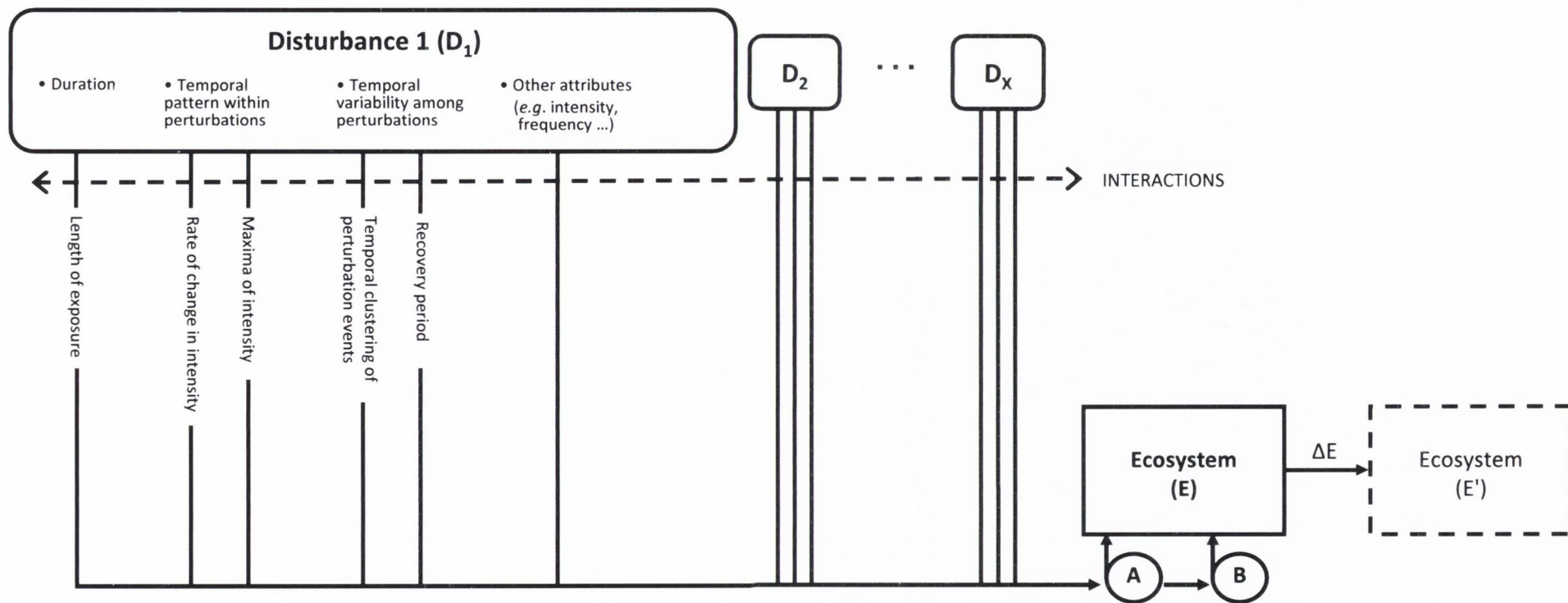


Fig. 5.1. Generalised conceptual model representing the manner by which a disturbance regime composed of multiple agents of disturbance affects an ecosystem, causing a shift (ΔE) in its state driven by changes in its (A) abiotic and (B) biotic components.

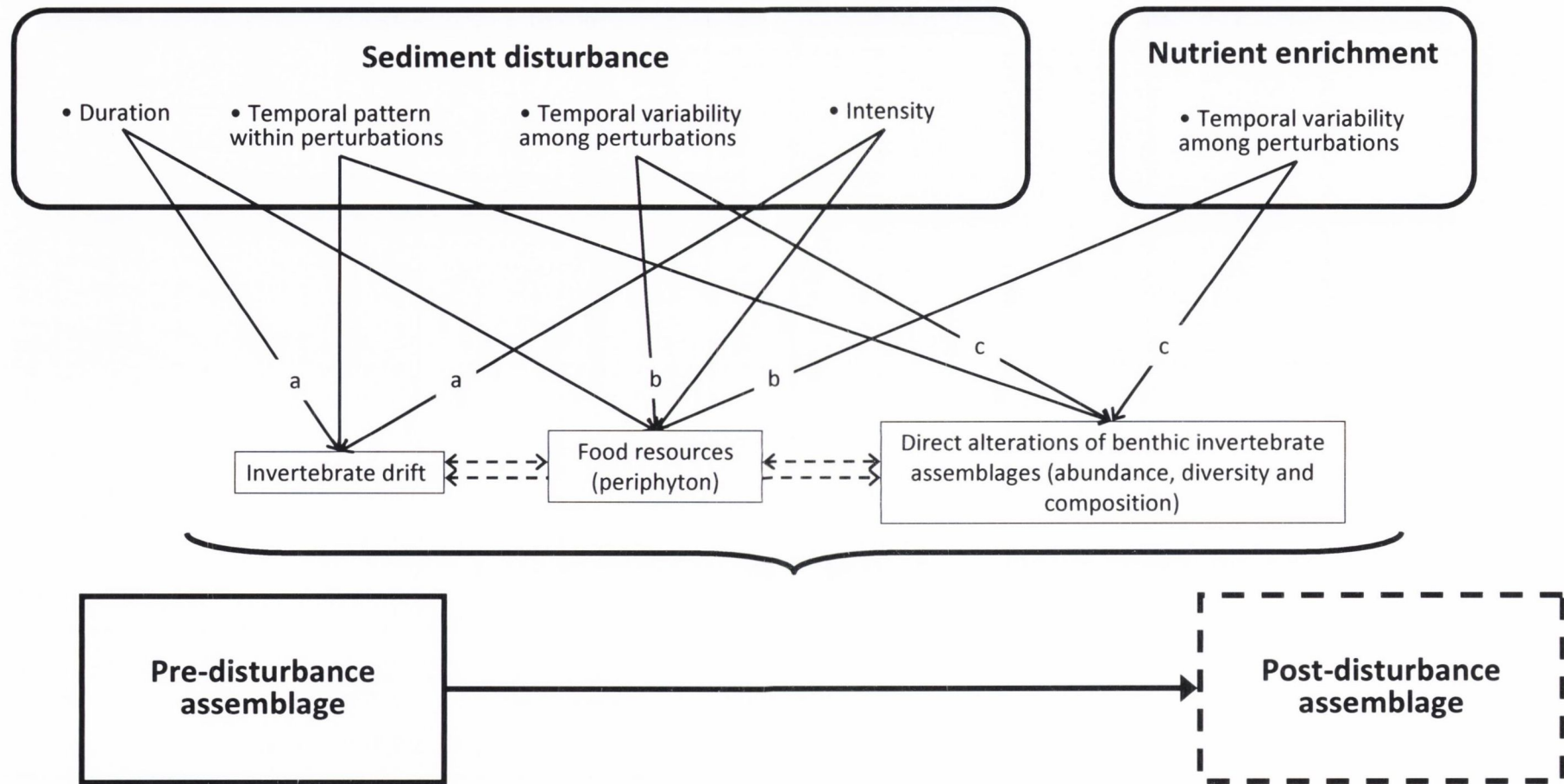


Fig. 5.2. Schematic representation of direct (closed lines) and indirect (dashed lines) effects of sediment disturbance temporal properties on stream biota. Lines sharing the same letter represent an interactive effect among corresponding properties.

All temporal properties of disturbances tested experimentally demonstrated a capacity to mediate the extent and type of responses of biotic assemblages through different but complementary mechanisms (Fig. 5.2). These mechanisms were unconfounded from the effects of other disturbance traits by my experimental designs. The observed effects of temporal properties were often specific to the response variable under consideration even for those descriptors of the same biological component (*e.g.* periphyton, benthic invertebrates). Moreover, my work stresses the existence of important novel causal mechanisms; disturbance effects involved interactions of temporal properties with other disturbance traits (Chapter II) and additional stressors (Chapter IV). These results suggest strongly a much more complex role of these properties in the definition of disturbance effects than that attributable to their relative individual effects. They also open promising new research opportunities.

Overall, my results provide proof of the mechanistic mediation of different temporal attributes on the short term effects of disturbances on local ecosystem processes. Prediction of the causes and consequences of global environmental change requires, however, the hierarchical integration of phenomena that occur at different scales of space, time, and ecological organisation (Levin 1992, Wu 1995, Huston 1999, Wilbanks and Kates 1999, Lowe *et al.* 2006). There is, therefore, a need for future research to investigate and integrate the consequences of these mechanisms at different scales. Theory has suggested, for example, that mechanisms leading to long-term, stable species coexistence can operate in a strictly temporal dimension, without a spatial component, if they allow disturbed organisms to exploit disturbance-induced temporal variability ('temporal niche differentiation'; Wilson 1990). This idea is important because it recognises temporal variability as an independent determinant of biodiversity patterns

(Chesson and Huntly 1997). Roxburgh *et al.* (2004) demonstrated the applicability of this concept to the ('within-patch') Intermediate Disturbance Hypothesis using frequency as the force enhancing purely temporal mechanisms of species coexistence. My results suggest, however, that temporal attributes other than frequency can also provide alternative mechanisms of ecological differentiation (Fig. 5.1), therefore generating potential further opportunities for species coexistence.

Important practical implications for environmental monitoring and conservation can also be drawn from my work. Quality standards and permit limits enforced by environmental legislation to preserve natural ecosystems are normally based either on acute (*e.g.* daily maximum) or chronic (*e.g.* monthly average) criteria. However, these criteria may not be appropriate for typical environmental stressors, which are often episodic or variable. My findings suggest that neither the average nor the maximum intensity comprise adequate measures as different responses to disturbance appear to develop under varying conditions of duration (Chapter II), and temporal variability both within (Chapter III) and among (Chapter IV) perturbation events. A simple integrated measure such as the dose of a perturbation (intensity \times duration) may also not be adequate for the same reason. Future research should, therefore, include as one of its goals the development of much improved guidance for sampling and characterising the temporal characteristics of disturbances. The importance of detecting and incorporating environmental variability into management and conservation practices is an open debate for scientists and managers (Irvine 2004, Donohue *et al.* 2005, Knowlton and Jones 2006, Diez *et al.* 2009). On the one hand, managers need to begin planning with urgency for adaptation to the increasing complexity of our understanding of the effects of anthropogenic impacts on ecosystems (Paine *et al.* 1998, Benedetti-Cecchi *et al.* 2006, Liu *et al.* 2007, Klok and

Kraak 2008, Bozelli *et al.* 2009), whereas on the other hand, however, experience demonstrates that this adaptation is often hindered in practice by its complexity and cost-benefit limitations, although the application of novel technologies may give a practical solution to this problem in the future (*e.g.* Gupta *et al.* 2006, Onderka and Pekárová 2008, Bierman *et al.* In Press). Nonetheless, examples of recommendations for evaluating environmental quality criteria on the basis of temporal variability already exist (*e.g.* U.S. EPA 1991) and work to implement them into management through the use of dynamic models has been done (*e.g.* Diamond and Butcher 2003). Flexibility is required to move towards more accurate and cost-effective management and conservation practices. Conventional steady-state approaches could be used, for example, in situations where risk to degradation is considered to be low and where sacrificing detail and potential accuracy can be done with an acceptable margin of error. For that to happen, disturbance ecology needs to become more predictive, and the predictions need to be more robust. For any particular type of disturbance, research should be designed to distinguish the effects of its constituent properties on a suite of biotic and abiotic attributes through continuous shifting between large- and small-scale studies (Root and Schneider 1995). Information gained from field studies in which continuous environmental monitoring is combined with regular biological sampling can, for example, shed light on possible causal trends driven by temporal variability in environmental conditions (*e.g.* Hewitt and Norkko 2007, Yuan 2010). Observed trends can be tested subsequently by appropriate experimental designs to elucidate causal mechanisms. In due course, this information will eventually enhance predictive model fitting by allowing the models to converge to effects derived from the time course of disturbances. This procedure will ultimately help achieve better conservation practices

by refining the understanding of ecosystem responses to disturbances under realistic temporal scenarios and better inform future implementations of stressor-specific criteria.

In conclusion, the experimental work described in this thesis demonstrates how the temporal profile of a disturbance regime can mediate biological responses independently of the magnitude or extent of the disturbance. This process is facilitated by different mechanisms involving both direct ('immediate') and indirect ('delayed') alterations of biotic and abiotic components of disturbed ecosystems. The temporal pattern of disturbances regulated both the type and extent of responses and involved interactions with other disturbance traits and stressors. These findings highlight the importance of the temporal dimension of disturbances in ecology and emphasise the necessity of its integration into the study, prediction and management of environmental disturbances in an increasingly complex humanised environment.

References



Effluent discharge: a clear example of a temporally variable pulsed perturbation
(photo by U.S. Department of Agriculture)

- Adler, P. B., D. A. Raff, and W. K. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465-479.
- Airolidi, L. 1998. Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. *Ecology* 79: 2759-2770.
- Airolidi, L. 2000. Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs. *Marine Ecology Progress Series* 195: 81-92.
- Airolidi, L., D. Balata, and M. W. Beck. 2008. The Gray Zone: relationships between habitat loss and marine diversity and their applications in conservation. *Journal of Experimental Marine Biology and Ecology* 366: 8-15.
- Alabaster, J. S. 1972. Suspended solids and fisheries. *Proceedings of the Royal Society of London B* 180: 395-406.
- Alados, C. L., Y. Pueyo, J. Escós, and A. Andujar. 2009. Effects of the spatial pattern of disturbance on the patch-occupancy dynamics of juniper-pine open woodland. *Ecological Modelling* 220: 1544-1550.
- Aldridge, D. W., B. S. Payne, and A. C. Miller. 1987. The effects of intermittent exposure to suspended solids and turbulence on three species of freshwater mussels. *Environmental Pollution* 45: 17-28.
- Allan, J. D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 35: 257-284.
- Anderson, H. W., M. D. Hoover, and K. G. Reinhart. 1976. *Forest and Water: Effects of Forest Management on Floods, Sediment and Water Supply*. USDA Forest Service General Technical Report PSW-18. Forest Service, US Department of Agriculture, Berkeley, California.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32-46.
- Anderson, M. J. and C. J. F. Ter Braak. 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* 73: 85.
- Anderson, M. J. and R. N. Gorley. 2007. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E, Plymouth.

- Atalah, J., S. A. Otto, M. J. Anderson, M. J. Costello, M. Lenz, and M. Wahl. 2007. Temporal variance of disturbance did not affect diversity and structure of a marine fouling community in north-eastern New Zealand. *Marine Biology* 157: 199–211.
- Attayde, J. L. and L.-A. Hansson. 2001. Press perturbation experiments and the indeterminacy of ecological interactions: effects of taxonomic resolution and experimental duration. *Oikos* 92: 235–244.
- Azim, M. E. and T. Asaeda. 2005. Periphyton structure, diversity and colonisation. Pages 15–33 in M. E. Azim, M. C. J. Verdegem, A. A. van Dam, and M. C. M. Beveridge, editors. *Periphyton: Ecology, Exploitation and Management*. CABI Publishing, Wallingford, Oxfordshire.
- Banas, D., G. Masson, L. Leglise, P. Usseglio-Polatera, and C. E. Boyd. 2008. Assessment of sediment concentration and nutrient loads in effluents drained from extensively managed fishponds in France. *Environmental Pollution* 152: 679–685.
- Barton, D. R. and M. E. D. Farmer. 1997. The effects of conservation tillage practices on benthic invertebrate communities in headwater streams in southwestern Ontario, Canada. *Environmental Pollution* 96: 207–215.
- Bascompte, J. and R. V. Solé. 1998. Effects of habitat destruction in a prey-predator metapopulation model. *Journal of Theoretical Biology* 195: 383–393.
- Bell, G. 2001. Neutral macroecology. *Science* 293: 2413–2418.
- Bell, T., W. E. Neill, and D. Schluter. 2003. The effect of temporal scale on the outcome of trophic cascade experiments. *Oecologia* 134: 578–586.
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65: 1–13.
- Benedetti-Cecchi, L. 2000. Variance in ecological consumer-resource interactions. *Nature* 407: 370–374.
- Benedetti-Cecchi, L. 2003. The importance of the variance around the mean effect size of ecological processes. *Ecology* 84: 2335–2346.
- Benedetti-Cecchi, L., S. Vaselli, E. Maggi, and I. Bertocci. 2005. Interactive effects of spatial variance and mean intensity of grazing on algal cover in rock pools. *Ecology* 86: 2212–2222.

- Benedetti-Cecchi, L., I. Bertocci, S. Vaselli, and E. Maggi. 2006. Temporal variance reverses the impact of high mean intensity of stress in climate change experiments. *Ecology* 87: 2489-2499.
- Bengtsson, J., S. G. Nilsson, A. Franc, and P. Menozzi. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management* 132: 39-50.
- Berg, L. and T. G. Northcote. 1985. Changes in territorial, gill-flaring, and feeding behaviour in juvenile Coho salmon (*Oncorhynchus kisutch*) following short-term pulses of suspended sediment. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1410-1417.
- Berkman, H. E. and C. F. Rabeni. 1987. Effect of siltation on stream fish communities. *Environmental Biology of Fishes* 18: 285-294.
- Bertocci, I., E. Maggi, S. Vaselli, and L. Benedetti-Cecchi. 2005. Contrasting effects of mean intensity and temporal variation of disturbance on a rocky seashore. *Ecology* 86: 2061-2067.
- Bertocci, I., S. Vaselli, E. Maggi, and L. Benedetti-Cecchi. 2007. Changes in temporal variance of rocky shore organism abundances in response to manipulation of mean intensity and temporal variability of aerial exposure. *Marine Ecology Progress Series* 338: 11-20.
- Bierman, P., M. Lewis, B. Ostendorf, and J. Tanner. In Press. A review of methods for analysing spatial and temporal patterns in coastal water quality. *Ecological Indicators* doi:10.1016/j.ecolind.2009.11.001
- Biggs, B. J. F. and H. A. Thomsen. 1995. Disturbances in stream periphyton by perturbations in shear stress: time to structural failure and differences in community resistance. *Journal of Phycology* 31: 233-241.
- Bo, T., F. Stefano, G. Malacarne, M. Pessino, and F. Sgariboldi. 2007. Effects of clogging on stream macroinvertebrates: an experimental approach. *Limnologica - Ecology and Management of Inland Waters* 37: 186-192.
- Boles, G. R. 1981. Macroinvertebrate colonization of replacement substrate below a hypolimnial release reservoir. *Hydrobiologia* 78: 133-146.

- Bond, N. R. and B. J. Downes. 2003. The independent and interactive effects of fine sediment and flow on benthic invertebrate communities characteristic of small upland streams. *Freshwater Biology* 48: 455-465.
- Botta, A. and J. A. Foley. 2002. Effects of climate variability and disturbances on the Amazonian terrestrial ecosystems dynamics. *Global Biogeochemical Cycles* 16: 1070.
- Boubée, J. A. T., T. L. Dean, D. W. West, and R. F. G. Barrier. 1997. Avoidance of suspended sediment by the juvenile migratory stage of six New Zealand native fish species. *New Zealand Journal of Marine and Freshwater Research* 31: 61-69.
- Bozelli, R. L., A. Caliman, R. D. Guariento, L. S. Carneiro, J. M. Santangelo, M. P. Figueiredo-Barros, J. J. F. Leal, A. M. Rocha, L. B. Quesado, P. M. Lopes, V. F. Farjalla, C. C. Marinho, F. Roland, and F. A. Esteves. 2009. Interactive effects of environmental variability and human impacts on the long-term dynamics of an Amazonian floodplain lake and a South Atlantic coastal lagoon. *Limnologica - Ecology and Management of Inland Waters* 39: 306-313.
- Bracken, M. E. S., S. E. Friberg, C. A. Gonzalez-Dorantes, and S. L. Williams. 2008. Functional consequences of realistic biodiversity changes in a marine ecosystem. *Proceedings of the National Academic of Sciences of the United States of America* 105: 924-928.
- Brawn, J. D., S. K. Robinson, and R. T. Frank, III. 2001. The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32: 251-276.
- Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* 27: 326-349.
- Breitburg, D. L., J. W. Baxter, C. A. Hatfield, R. W. Howarth, C. G. Jones, G. M. Lovett, and C. Wigand. 1998. Understanding effects of multiple stressors: ideas and challenges. Pages 416-431 in M. L. Pace and P. M. Groffman, editors. *Successes, Limitations, and Frontiers in Ecosystem Science*. Springer, New York.
- Brittain, E. J. and T. J. Eikeland. 1988. Invertebrate drift: a review. *Hydrobiologia* 166: 77-93.
- Broekhuizen, N., S. Parkyn, and D. Miller. 2001. Fine sediment effects on feeding and growth in the invertebrate grazers *Potamopyrgus antipodarum* (Gastropoda, Hydrobiidae) and *Deleatidium* sp. (Ephemeroptera, Leptophlebiidae). *Hydrobiologia* 457: 125-132.
- Bruton, M. N. 1985. The effects of suspensoids on fish. *Hydrobiologia* 125: 221-241.

- Bunge, J. and M. Fitzpatrick. 1993. Estimating the number of species: a review. *Journal of the American Statistical Association* 88: 364-373.
- Burkholder, J. M. and B. E. Coker. 1991. Response of periphyton communities to clay and phosphate loading in a shallow reservoir. *Journal of Phycology* 27: 373-384.
- Butler, M. J., IV. 1989. Community responses to variable predation: field studies with sunfish and freshwater macroinvertebrates. *Ecological Monographs* 59: 311-328.
- Cambray, J. A. 1983. Early development and larval behaviour of a minnow, *Barbus anoplus* (Pisces: Cyprinidae). *South African Journal of Zoology* 18: 331-336.
- Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* 8: 559-568.
- Caswell, H. and J. E. Cohen. 1995. Red, white and blue: environmental variance spectra and coexistence in metapopulations. *Journal of Theoretical Biology* 176: 301-316.
- Chamberlin, T. W., R. D. Hart, and F. H. Everest. 1991. Timber harvesting, silviculture, and watershed processes. Pages 181-206 in W. R. Meehan, editor. *Influences of Forest and Rangeland Management*. American Fisheries Society Special Publication 19, Bethesda, Maryland.
- Chapin, F. S., III, K. Autumn, and F. Pugnaire. 1993. Evolution of suites of traits in response to environmental stress. *The American Naturalist* 142: S78-S92.
- Chapin, F. S., III, B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. *Science* 277: 500-504.
- Chapin, F. S., III, E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. *Nature* 405: 234.
- Chase, J. M. and M. A. Leibold. 2003. *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago, IL.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America* 104: 17430-17434.

- Chave, J., H. C. Muller-Landau, and A. L. Simon. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *The American Naturalist* 159: 1-23.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* 7: 241-253.
- Chesson, P. 1994. Multispecies competition in variable environments. *Theoretical Population Biology* 45: 227-276.
- Chesson, P. and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist* 150: 519-553.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-366.
- Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theoretical Population Biology* 28: 263-287.
- Chesson, P. L. 1986. Environmental variation and the coexistence of species. Pages 240-256 in T. J. Case, editor. *Community Ecology*. Harper and Row Publishers, New York, NY.
- Chivian, E. 2001. Environment and health: 7. Species loss and ecosystem disruption - the implications for human health. *Canadian Medical Association Journal* 164: 66-69.
- Christensen, J. H. and O. B. Christensen. 2003. Climate modelling: severe summertime flooding in Europe. *Nature* 421: 805.
- Chutter, F. M. 1969. The effects of silt and sand on the invertebrate fauna of streams and rivers. *Hydrobiologia* 34: 57-76.
- Ciborowski, J. J. H., P. J. Pointing, and L. D. Corkum. 1977. The effect of current velocity and sediment on the drift of the mayfly *Ephemerella subvaria* McDunnough. *Freshwater Biology* 7: 567-572.
- Cifuentes, M., C. Kamlah, M. Thiel, M. Lenz, and M. Wahl. 2007. Effects of temporal variability of disturbance on the succession in marine fouling communities in northern-central Chile. *Journal of Experimental Marine Biology and Ecology* 352: 280-294.
- Clark, J. S. 1996. Testing disturbance theory with long-term data: alternative life-history solutions to the distribution of events. *The American Naturalist* 148: 976-996.

- Clarke, K. R. and R. M. Warwick. 2001. Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation. PRIMER-E, Plymouth.
- Clesceri, L. S., A. E. Greenberg, and A. D. Eaton, editors. 1999. Standard Methods for the Examination of Water and Wastewater. 20th edition. American Public Health Association, American Water Works Association and Water Environment Federation, Washington, D.C.
- Cline, L. D., R. A. Short, and J. V. Ward. 1982. The influence of highway construction on the macroinvertebrates and periphytic algae of a high mountain stream. *Hydrobiologia* 96: 149-159.
- Cohen, A. S. 1995. Paleoecological approaches to the conservation biology of benthos in ancient lakes: a case study from Lake Tanganyika. *Journal of the North American Benthological Society* 14: 654-668.
- Collins, B., G. Wein, and T. Philippi. 2001. Effects of disturbance intensity and frequency on early old-field succession. *Journal of Vegetation Science* 12: 721-728.
- Collins, S. L. 1992. Fire frequency and community heterogeneity in tallgrass prairie vegetation. *Ecology* 73: 2001-2006.
- Collins, S. L. 2000. Disturbance frequency and community stability in native tallgrass prairie. *The American Naturalist* 155: 311-325.
- Collins, S. L. and M. D. Smith. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology* 87: 2058-2067.
- Coman, G. J., M. J. Sellars, and D. T. Morehead. 2005. Toxicity of ozone generated from different combinations of ozone concentration (C) and exposure time (T): a comparison of the relative effect of C and T on hatch rates of *Penaeus* (Marsupenaeus) *japonicus* embryos. *Aquaculture* 244: 141-145.
- Condit, R., P. Ashton, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, C. Ewango, R. Foster, I. A. U. N. Gunatilleke, C. V. S. Gunatilleke, P. Hall, K. E. Harms, T. Hart, C. Hernandez, S. Hubbell, A. Itoh, S. Kiratiprayoon, J. LaFrankie, S. L. de Lao, J.-R. Makana, M. N. S. Noor, A. R. Kassim, S. Russo, R. Sukumar, C. Samper, H. S. Suresh, S. Tan, S. Thomas, R. Valencia, M. Vallejo, G. Villa, and T. Zillio. 2006. The importance of demographic niches to tree diversity. *Science* 313: 98-101.

- Confer, J. L., G. L. Howick, M. H. Corzette, S. L. Kramer, S. Fitzgibbon, and R. Landesberg. 1978. Visual predation by planktivores. *Oikos* 31: 27-37.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Connolly, N. M. and R. G. Pearson. 2007. The effect of fine sedimentation on tropical stream macroinvertebrate assemblages: a comparison using flow through artificial stream channels and recirculating mesocosms. *Hydrobiologia* 592: 423-438.
- Coors, A. and L. D. Meester. 2008. Synergistic, antagonistic and additive effects of multiple stressors: predation threat, parasitism and pesticide exposure in *Daphnia magna*. *Journal of Applied Ecology* 45: 1820-1828.
- Costanza, R. and R. D'Arge. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253.
- Crain, C. M., K. Kroeker, and B. S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11: 1304-1315.
- Crawley, M. J. 2004. Timing of disturbance and coexistence in a species-rich ruderal plant community. *Ecology* 85: 3277-3288.
- Cristoni, C., M. A. Colangelo, and V. U. Ceccherelli. 2004. Spatial scale and meiobenthic copepod recolonisation: testing the effect of disturbance size in a seagrass habitat. *Journal of Experimental Marine Biology and Ecology* 298: 49-70.
- Crosa, G., E. Castelli, G. Gentili, and P. Espa. 2010. Effects of suspended sediments from reservoir flushing on fish and macroinvertebrates in an alpine stream. *Aquatic Sciences - Research Across Boundaries* 72: 85-95.
- Crouse, M. R., C. A. Callahan, K. W. Malueg, and S. E. Dominguez. 1981. Effects of fine sediments on growth of juvenile coho salmon in laboratory streams. *Transactions of the American Fisheries Society* 110: 281-286.
- Crowl, T. A. 1989. Effects of crayfish size, orientation, and movement on the reaction distance of largemouth bass foraging in clear and turbid water. *Hydrobiologia* 183: 133-140.
- Crutzen, P. J. 2002. Geology of mankind. *Nature* 415: 23.
- Cuker, B. E. 1987. Field experiment on the influences of suspended clay and P on the plankton of a small lake. *Limnology and Oceanography* 32: 840-847.

- Cuker, B. E., P. T. Gama, and J. M. Burkholder. 1990. Type of suspended clay influences lake productivity and phytoplankton community response to phosphorus loading. *Limnology and Oceanography* 35: 830-839.
- Cuker, B. E. and L. Hudson. 1992. Type of suspended clay influences zooplankton response to phosphorus loading. *Limnology and Oceanography* 37: 566-576.
- Culp, J. M., F. J. Wrona, and R. W. Davies. 1986. Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology* 64: 1345-1351.
- Culp, J. M., F. J. Wrona, and R. W. Davies. 1987. Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology* 64: 1345-1351.
- Cummins, K. W. 1975. Macroinvertebrates. Pages 170-198 in B. A. Whitton, editor. *River Ecology*. Blackwell, Oxford.
- Cummins, K. W. and M. J. Klug. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 10: 147-172.
- Dahlberg, A., J. Schimmel, A. F. S. Taylor, and H. Johannesson. 2001. Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. *Biological Conservation* 100: 151-161.
- Davey, G. W., T. J. Doeg, and J. D. Blyth. 1987. Changes in benthic sediment in the Thomson River, Southeastern Australia, during construction of the Thomson Dam. *Regulated Rivers: Research & Management* 1: 71-84.
- Davies-Colley, R. J., C. W. Hickey, J. M. Quinn, and P. A. Ryan. 1992. Effects of clay discharges on streams 1. Optical properties and periphyton. *Hydrobiologia* 248: 215-234.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351-389.
- Dayton, P. K., V. Currie, T. Gerrodette, B. D. Keller, R. Rosenthal, and D. V. Tresca. 1984. Patch dynamics and stability of some California kelp communities. *Ecological Monographs* 54: 254-289.

- De Robertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Canadian Journal of Fisheries and Aquatic Science* 60: 1517-1526.
- Dearing, J. A. and R. T. Jones. 2003. Coupling temporal and spatial dimensions of global sediment flux through lake and marine sediment records. *Global and Planetary Change* 39: 147-168.
- Diamond, J. and J. B. Butcher. 2003. Effluent Limits for Fluctuating Discharges: Alternate Frameworks for Water Quality Criteria Incorporating Chemical Frequency, Magnitude, and Duration. Project 98-HHE-3; Water Environment Research Foundation, Alexandria, VA.
- Diamond, J. M., S. J. Klaine, and J. B. Butcher. 2006. Implications of pulsed chemical exposures for aquatic life criteria and wastewater permit limits. *Environmental Science and Technology* 40: 5132-5138.
- Diez, J. M., H. L. Buckley, B. S. Case, M. A. Harsch, A. R. Sciligo, S. R. Wangen, and R. P. Duncan. 2009. Interacting effects of management and environmental variability at multiple scales on invasive species distributions. *Journal of Applied Ecology* 46: 1210-1218.
- Doeg, T. J. and G. A. Milledge. 1991. Effect of experimentally increasing concentrations of suspended solids on macroinvertebrate drift. *Australian Journal of Marine and Freshwater Research* 42: 519-526.
- Doeg, T. J. and J. D. Koehn. 1994. Effects of draining and desilting a small weir on downstream fish and macroinvertebrates. *Regulated Rivers: Research & Management* 9: 263-277.
- Donohue, I., R. W. Duck, and K. Irvine. 2003a. Land use, sediment loads and dispersal pathways from two catchments at the southern end of Lake Tanganyika, Africa: implications for lake management. *Environmental Geology* 44: 448-455.
- Donohue, I. and K. Irvine. 2003. Effects of sediment particle size composition on survivorship of benthic invertebrates from Lake Tanganyika, Africa. *Archiv für Hydrobiologie* 157: 131-144.
- Donohue, I., E. Verheyen, and K. Irvine. 2003b. *In situ* experiments on the effects of increased sediment loads on littoral rocky shore communities in Lake Tanganyika, East Africa. *Freshwater Biology* 48: 1603-1616.
- Donohue, I. and K. Irvine. 2004a. Seasonal patterns of sediment loading and benthic invertebrate community dynamics in Lake Tanganyika, Africa. *Freshwater Biology* 49: 320-331.

- Donohue, I. and K. Irvine. 2004b. Size-specific effects of increased sediment loads on gastropod communities in Lake Tanganyika, Africa. *Hydrobiologia* 522: 337-342.
- Donohue, I., D. Styles, C. Coxon, and K. Irvine. 2005. Importance of spatial and temporal patterns for assessment of risk of diffuse nutrient emissions to surface waters. *Journal of Hydrology* 304: 183-192.
- Donohue, I. and J. García Molinos. 2009. Impacts of increased sediment loads on the ecology of lakes. *Biological Reviews* 84: 517-531.
- Donohue, I., A. L. Jackson, M. T. Pusch, and K. Irvine. 2009. Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales. *Ecology* 90: 3470-3477.
- Doull, J. and K. K. Rozman. 2000. Using Haber's Law to define the margin of exposure. *Toxicology* 149: 1-2.
- Downes, B. J., P. S. Lake, A. Glaister, and N. R. Bond. 2006. Effects of sand sedimentation on the macroinvertebrate fauna of lowland streams: are the effects consistent? *Freshwater Biology* 51: 144-160.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81: 163-182.
- Effenberger, M., G. Sailer, C. R. Townsend, and C. D. Matthaei. 2006. Local disturbance history and habitat parameters influence the microdistribution of stream invertebrates. *Freshwater Biology* 51: 312-332.
- Effenberger, M., J. Engel, S. Diehl, and C. Matthaei. 2008. Disturbance history influences the distribution of stream invertebrates by altering microhabitat parameters: a field experiment. *Freshwater Biology* 53: 996-1011.
- Eisenreich, S. J., R. T. Bannerman, and D. E. Armstrong. 1975. A simplified phosphorus analysis technique. *Environmental Letters* 9: 43-53.
- Elliot, W. J. 2006. The roles of natural and human disturbances in forest soil erosion. Pages 177-185 in P. N. Owens and A. J. Collins, editors. *Soil Erosion and Sediment Redistribution in River Catchments*. Commonwealth Agricultural Bureau International, Wallingford, Oxfordshire.

- Elliott, J. A., A. E. Irish, and C. S. Reynolds. 2001. The effects of vertical mixing on a phytoplankton community: a modelling approach to the intermediate disturbance hypothesis. *Freshwater Biology* 46: 1291-1297.
- Ellis, M. M. 1936. Erosion silt as a factor in aquatic environments. *Ecology* 17: 29-42.
- Ellwood, M. D. F., A. Manica, and W. A. Foster. 2009. Stochastic and deterministic processes jointly structure tropical arthropod communities. *Ecology Letters* 12: 277-284.
- Enberg, K., M. S. Fowler, and E. Ranta. 2006. The impacts of different management strategies and environmental forcing in ecological communities. *Proceedings of the Royal Society of London B* 273: 2491-2499.
- Erb, K.-H., F. Krausmann, V. Gaube, S. Gingrich, A. Bondeau, M. Fischer-Kowalski, and H. Haberl. 2009. Analyzing the global human appropriation of net primary production - processes, trajectories, implications. An introduction. *Ecological Economics* 69: 250-259.
- Erman, D. C. and N. A. Erman. 1984. The response of stream macroinvertebrates to substrate size and heterogeneity. *Hydrobiologia* 108: 75-82.
- Extence, C. A. 1978. The effects of motorway construction on an urban stream. *Environmental Pollution* 17: 245-252.
- Ferrier, R. C., A. C. Edwards, D. Hirst, I. G. Littlewood, C. D. Watts, and R. Morris. 2001. Water quality of Scottish rivers: spatial and temporal trends. *Science of the Total Environment* 265: 327-342.
- Finger, D., P. Bossard, M. Schmid, L. Jaun, B. Müller, D. Steiner, E. Schäffer, M. Zeh, and A. Wüest. 2007. Effects of alpine hydropower operations on primary production in a downstream lake. *Aquatic Science* 69: 240-256.
- Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52: 93-110.
- Flather, C. H. and M. Bevers. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist* 159: 40-56.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C.

- Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. *Science* 309: 570-574.
- Folt, C. L., C. Y. Chen, M. V. Moore, and J. Burnaford. 1999. Synergism and antagonism among multiple stressors. *Limnology and Oceanography* 44: 864-877.
- Francoeur, N. S. and B. J. F. Biggs. 2006. Short-term effects of elevated velocity and sediment abrasion on benthic algal communities. *Hydrobiologia* 561: 59-69.
- Fraterrigo, J. M. and J. A. Rusak. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. *Ecology Letters* 11: 756-770.
- Fritz, K. M., W. K. Dodds, and J. Pontius. 1999. The effects of bison crossings on the macroinvertebrate community in a tallgrass prairie stream. *The American Midland Naturalist* 141: 253-265.
- Fritz, K. M. and W. K. Dodds. 2005. Harshness: characterisation of intermittent stream habitat over space and time. *Marine and Freshwater Research* 56: 13-23.
- Froelich, P. N. 1988. Kinetic control of dissolved phosphate in natural rivers and estuaries: a primer on the phosphate buffer mechanism. *Limnology and Oceanography* 33: 649-668.
- Fukami, T. 2001. Sequence effects of disturbance on community structure. *Oikos* 92: 215-224.
- Furniss, M. J., T. D. Roelofs, and C. S. Yee. 1991. Road construction and maintenance. Pages 297-323 in W. R. Meehan, editor. *Influences of Forest and Rangeland Management*. American Fisheries Society Special Publication 19, Bethesda, Maryland.
- Galbraith, R. V., E. A. MacIsaac, J. S. Macdonald, and A. P. Farrell. 2006. The effect of suspended sediment on fertilization success in sockeye (*Oncorhynchus nerka*) and coho (*Oncorhynchus kisutch*) salmon. *Canadian Journal of Fisheries and Aquatic Science* 63: 2487-2494.
- García Molinos, J. and I. Donohue. 2009. Differential contribution of concentration and exposure time to sediment dose effects on stream biota. *Journal of the North American Benthological Society* 28: 110-121.
- Gardener, D. E., F. J. Miller, E. J. Blommer, and D. L. Coffin. 1979. Influence of exposure mode on the toxicity of NO₂. *Environmental Health Perspectives* 30: 23-29.

- Gardner, M. B. 1981. Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. *Ecology* 62: 571-578.
- Gaston, K. J. and B. H. McArdle. 1993. Measurement of variation in the size of populations in space and time: some points of clarification. *Oikos* 68: 357-360.
- Gibbins, C., D. Vericat, and R. J. Batalla. 2007a. When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. *Freshwater Biology* 52: 2369-2384.
- Gibbins, C., D. Vericat, R. J. Batalla, and C. M. Gomez. 2007b. Shaking and moving: low rates of sediment transport trigger mass drift of stream invertebrates. *Canadian Journal of Fisheries and Aquatic Science* 64: 1-5.
- Gilmour, J. P. 2002. Acute sedimentation causes size-specific mortality and asexual budding in the mushroom coral, *Fungia fungites*. *Marine and Freshwater Research* 53: 805-812.
- Glasby, T. M. and A. J. Underwood. 1996. Sampling to differentiate between pulse and press perturbations. *Environmental Monitoring and Assessment* 42: 241-252.
- Goldberg, D. E. and K. L. Gross. 1988. Disturbance regimes of mid-successional old fields. *Ecology* 69: 1677-1688.
- Goldman, J. C. 1986. On phytoplankton growth rates and particulate C:N:P ratios at low light. *Limnology and Oceanography* 31: 1358-1363.
- Graham, A. A. 1990. Siltation of stone-surface periphyton in rivers by clay-sized particles from low concentrations in suspension. *Hydrobiologia* 199: 107-115.
- Gregg, J. C., J. W. Fleeger, and K. R. Carman. 1997. Effects of suspended, diesel-contaminated sediment on feeding rate in the darter goby, *Gobionellus boleosoma* (Teleostei: Gobiidae). *Marine Pollution Bulletin* 34: 269-275.
- Gregory, R. S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries Aquatic Science* 50: 241-246.
- Gregory, R. S. and T. G. Northcote. 1993. Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 233-240.

- Groffman, P., J. Baron, T. Blett, A. Gold, I. Goodman, L. Gunderson, B. Levinson, M. Palmer, H. Paerl, G. Peterson, N. Poff, D. Rejeski, J. Reynolds, M. Turner, K. Weathers, and J. Wiens. 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? *Ecosystems* 9: 1-13.
- Gupta, P., S. A. Christopher, J. Wang, R. Gehrig, Y. Lee, and N. Kumar. 2006. Satellite remote sensing of particulate matter and air quality assessment over global cities. *Atmospheric Environment* 40: 5880-5892.
- Haber, F. 1924. Zur geschichte des gaskrieges. Pages 76-92 in *Fünf Vorträge aus den Jahren 1920–1923*. Springer, Berlin.
- Haggard, B. E., E. H. Stanley, and D. E. Storm. 2005. Nutrient retention in a point-source-enriched stream. *Journal of the North American Benthological Society* 24: 29-47.
- Hannah, L., D. Lohse, C. Hutchinson, J. L. Carr, and A. Lankerani. 1994. A preliminary inventory of human disturbance of world ecosystems. *Ambio* 23: 246-250.
- Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. *Bioscience* 41: 382-392.
- Hansmann, E. W. and H. K. Phinney. 1973. Effects of logging on periphyton in coastal streams of Oregon. *Ecology* 54: 194-199.
- Harr, R. D., W. C. Harper, J. T. Krygier, and F. S. Hsieh. 1975. Changes in storm hydrographs after road building and clear-cutting in the Oregon Coast Range. *Water Resources Research* 11: 436-444.
- Harrison, A. D. and T. D. W. Farina. 1965. A naturally turbid water with deleterious effects on the egg capsules of planorbid snails. *Annals of Tropical Medicine and Parasitology* 59: 327-330.
- Haygarth, P. M. and S. C. Jarvis. 1997. Soil derived phosphorus in surface runoff from grazed grassland lysimeters. *Water Research* 31: 140-148.
- Heather, S., L. Mark, M. Markus, W. Martin, and C. T. Jeremy. 2008. The interaction between nutrient availability and disturbance frequency on the diversity of benthic marine communities on the north-east coast of England. *Journal of Animal Ecology* 77: 24-31.
- Herbert, W. M. and J. C. Merkens. 1961. The effect of suspended mineral solids on the survival of trout. *International Journal of Air and Water Pollution* 5: 46-55.

- Herbert, W. M. and J. M. Richards. 1963. The growth and survival of fish in some suspensions of solids of industrial origin. *International Journal of Air and Water Pollution* 7: 297-302.
- Heugens, E. H. W., A. J. Hendriks, T. Dekker, N. M. van Straalen, and W. Admiraal. 2002. A review of the effects of multiple stressors on aquatic organisms and analysis of uncertainty factors for use in risk assessment. *Critical Reviews in Toxicology* 31: 247-284.
- Hewitt, J. E. and J. Norkko. 2007. Incorporating temporal variability of stressors into studies: an example using suspension-feeding bivalves and elevated suspended sediment concentrations. *Journal of Experimental Marine Biology and Ecology* 341: 131-141.
- Hickman, K. R. and D. C. Hartnett. 2002. Effects of grazing intensity on growth, reproduction, and abundance of three palatable forbs in Kansas tallgrass prairie. *Plant Ecology* 159: 23-33.
- Hildebrand, S. G. 1974. The relation of drift to benthos density and food level in an artificial stream. *Limnology and Oceanography* 19: 951-957.
- Hillebrand, H. and U. Sommer. 1999. The nutrient stoichiometry of benthic microalgal growth: Redfield proportions are optimal. *Limnology and Oceanography* 44: 440-446.
- Hiura, T. 1995. Gap formation and species diversity in Japanese beech forests: a test of the intermediate disturbance hypothesis on a geographic scale. *Oecologia* 104: 265-271.
- Hoang, T. C., J. S. Gallagher, J. R. Tomasso, and S. J. Klaine. 2007. Toxicity of two pulsed metal exposures to *Daphnia magna*: relative effects of pulsed duration-concentration and influence of interpulse period. *Archives of Environmental Contamination and Toxicology* 53: 579-589.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4: 1-23.
- Horne, J. K. and D. C. Schneider. 1995. Spatial variance in ecology. *Oikos* 74: 18-26.
- Horner, R. R., E. B. Welch, M. R. Seeley, and J. M. Jacoby. 1990. Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration. *Freshwater Biology* 24: 215-232.
- Höss, S., M. Haitzer, W. Traunsperger, and C. E. W. Steinberg. 1999. Growth and fertility of *Caenorhabditis elegans* (Nematoda) in unpolluted freshwater sediments: response to

- particle size distribution and organic content. *Environmental Toxicology and Chemistry* 18: 2921-2925.
- Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Hubert, W. A., W. J. LaVoie, IV, and L. D. DeBray. 1996. Densities and substrate associations of macroinvertebrates in riffles of a small, high plains stream. *Journal of Freshwater Ecology* 11: 21-26.
- Hughes, F. M. R. and S. B. Rood. 2003. Allocation of river flows for restoration of floodplain forest ecosystems: a review of approaches and their applicability in Europe. *Environmental Management* 32: 12-33.
- Hughes, T. P. and J. H. Connell. 1999. Multiple stressors on coral reefs: a long-term perspective. *Limnology and Oceanography* 44: 932-940.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52: 577-586.
- Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist* 113: 81-101.
- Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86: 393-401.
- Hynes, H. B. N. 1970. *The Ecology of Running Waters*. The Blackburn Press, Caldwell, New Jersey.
- Imbert, J. B. and J. A. Perry. 2000. Drift and benthic invertebrate responses to stepwise and abrupt increases in non-scouring flow. *Hydrobiologia* 436: 191-208.
- Irvine, J. R. and P. R. Henriques. 1984. A preliminary investigation on effects of fluctuating flows on invertebrates of the Hawea River, a large regulated river in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 18: 283-290.
- Irvine, K. 2004. Classifying ecological status under the European Water Framework Directive: the need for monitoring to account for natural variability. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14: 107-112.
- Iwasa, Y. and S. A. Levin. 1995. The timing of life history events. *Journal of Theoretical Biology* 172: 33-42.

- Izagirre, O., A. Serra, H. Guasch, and A. Elosegi. 2009. Effects of sediment deposition on periphytic biomass, photosynthetic activity and algal community structure. *Science of the Total Environment* 407: 5694-5700.
- James, A. B. W., Z. S. Dewson, and R. G. Death. 2008. The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications* 24: 22-35.
- Johnson, E. A. 1992. *Fire and Vegetation Dynamics: Studies from the North American Boreal Forest*. Cambridge University Press, Cambridge.
- Johnson, E. A. and K. Miyanishi. 2007. *Plant Disturbance Ecology: the Process and the Response*. Elsevier Academic Press, Burlington, MA.
- Karr, J. R. and K. E. Freemark. 1985. Disturbance and vertebrates: an integrative perspective. Pages 153-168 in S. T. A. Pickett and P. S. White, editors. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Inc., Orlando, Florida.
- Kayhanian, M., C. Stransky, S. Bay, S.-L. Lau, and M. K. Stenstrom. 2008. Toxicity of urban highway runoff with respect to storm duration. *Science of the Total Environment* 389: 386-406.
- Kennard, D. K., K. Gould, F. E. Putz, T. S. Fredericksen, and F. Morales. 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. *Forest Ecology and Management* 162: 197-208.
- King, J. G. and L. C. Tennyson. 1984. Alteration of stream flow characteristics following road construction in north central Idaho. *Water Resources Research* 20: 1159-1163.
- Kirk, M. A. and S. A. Levin. 1996. The effects of disturbance architecture on landscape-level population dynamics. *Ecology* 77: 375-394.
- Klironomos, J. N., M. F. Allen, M. C. Rillig, J. Piotrowski, S. Makvandi-Nejad, B. E. Wolfe, and J. R. Powell. 2005. Abrupt rise in atmospheric CO₂ overestimates community response in a model plant-soil system. *Nature* 433: 621-624.
- Klok, C. and M. H. S. Kraak. 2008. Living in highly dynamic polluted river floodplains, do contaminants contribute to population and community effects? *Science of the Total Environment* 406: 455-461.

- Knight, H., S. Brandt, and M. R. Knight. 1998. A history of stress alters drought calcium signalling pathways in *Arabidopsis*. *The Plant Journal* 16: 681-687.
- Knowlton, M. F. and J. R. Jones. 2006. Temporal variation and assessment of trophic state indicators in Missouri reservoirs: implication for lake monitoring and management. *Lake and Reservoir Management* 22: 261 - 271.
- Kohler, S. L. 1992. Competition and the structure of a benthic stream community. *Ecological Monographs* 62: 165-188.
- Kondoh, M. 2001. Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society London B* 268: 269-271.
- Krause, P. R. 1995. Spatial and temporal variability in receiving water toxicity near an oil effluent discharge site. *Archives of Environmental Contamination and Toxicology* 29: 523-529.
- Krishnaswamy, J., M. Bunyan, V. K. Mehta, N. Jain, and K. U. Karanth. 2006. Impact of iron ore mining on suspended sediment response in a tropical catchment in Kudremukh, Western Ghats, India. *Forest Ecology and Management* 224: 187-198.
- Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19: 573-592.
- Lake, P. S. 2003. Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology* 48: 1161-1172.
- Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, A. D. Steinman, and C. D. McIntire. 1989. Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. *Ecology* 70: 1840-1856.
- Lande, R., S. Engen, and B.-E. Saether. 2003. *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford.
- Langsrud, Ø. 2003. ANOVA for unbalanced data: Use Type II instead of Type III sums of squares. *Statistics and Computing* 13: 163-167.
- Lawton, J. H. 1995. Ecological experiments with model systems. *Science* 269: 328-331.
- Ledger, M. E., R. M. L. Harris, A. M. Milner, and P. D. Armitage. 2006. Disturbance, biological legacies and community development in stream mesocosms. *Oecologia* 148: 682-691.

- Lehtiniemi, M., J. Engstrom-Ost, and M. Viitasalo. 2005. Turbidity decreases anti-predator behaviour in pike larvae, *Esox lucius*. *Environmental Biology of Fishes* 73: 1-8.
- Lemly, A. D. 1982. Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia* 87: 229-245.
- Lenat, D. R., D. I. Penrose, and K. W. Eagleson. 1981. Variable effects of sediment addition on stream benthos. *Hydrobiologia* 79: 187-194.
- Lenz, M., M. Molis, and M. Wahl. 2004a. Testing the intermediate disturbance hypothesis: response of fouling communities to various levels of emersion intensity. *Marine Ecology Progress Series* 278: 53-65.
- Lenz, M., M. Molis, and M. Wahl. 2004b. Experimental test of the intermediate disturbance hypothesis: frequency effects of emersion on fouling communities. *Journal of Experimental Marine Biology and Ecology* 305: 247-266.
- Levene, H. 1960. Robust tests for equality of variances. Pages 278-292 in I. Olkin, S.G. Ghurye, W. Hoeffding, W.G. Madow, and H. B. Mann, editors. *Contributions to Probability and Statistics: Essays in Honor of Harold Hotelling*. Stanford University Press, Menlo Park, California.
- Levin, D. A. 2004. Ecological speciation: The role of disturbance. *Systematic Botany* 29: 225-233.
- Levin, S. A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. *Ecology* 73: 1943-1967.
- Licursi, M. and N. Gómez. 2009. Effects of dredging on benthic diatom assemblages in a lowland stream. *Journal of Environmental Management* 90: 973-982.
- Lind, O. T. and L. Davalos-Lind. 1991. Association of turbidity and organic carbon with bacterial abundance and cell size in a large, turbid, tropical lake. *Limnology and Oceanography* 36: 1200-1208.
- Lind, O. T., T. H. Chrzanowski, and L. Davalos-Lind. 1997. Clay turbidity and the relative production of bacterioplankton and phytoplankton. *Hydrobiologia* 353: 1-18.
- Lind, O. T. 2003. Suspended clay's effect on lake and reservoir limnology. *Archiv für Hydrobiologie - Supplement* 193: 327-360.

- Lindenmayer, D. and M. A. McCarthy. 2002. Congruence between natural and human forest disturbance: a case study from Australian montane ash forests. *Forest Ecology and Management* 155: 319–335.
- Liu, J., T. Dietz, S. R. Carpenter, M. Alberti, C. Folke, E. Moran, A. N. Pell, P. Deadman, T. Kratz, J. Lubchenco, E. Ostrom, Z. Ouyang, W. Provencher, C. L. Redman, S. H. Schneider, and W. W. Taylor. 2007. Complexity of coupled human and natural systems. *Science* 317: 1513-1516.
- Lodge, D. M. and P. Kelly. 1985. Habitat disturbance and the stability of freshwater gastropod populations. *Oecologia* 68: 111-117.
- Loosanoff, V. L. and F. D. Tommers. 1948. Effects of suspended silt and other substances on rate of feeding of oysters. *Science* 107: 69-70.
- Lowe, J. A. and J. M. Gregory. 2005. The effects of climate change on storm surges around the United Kingdom. *Philosophical Transactions of the Royal Society A* 363: 1313-1328.
- Lowe, W. H., G. E. Likens, and M. E. Power. 2006. Linking scales in stream ecology. *Bioscience* 56: 591-597.
- Lubchenco, J. 1998. Entering the century of the environment: a new social contract for Science. *Science* 279: 491-497.
- Luttenton, M. R. and C. Baisden. 2006. The relationships among disturbance, substratum size and periphyton community structure. *Hydrobiologia* 561: 111-117.
- MacIsaac, H. J. and R. Rocha. 1995. Effects of suspended clay on zebra mussel (*Dreissena polymorpha*) faeces and pseudofaeces production. *Archiv für Hydrobiologie* 135: 53-64.
- Mailhot, A., S. Duchesne, D. Caya, and G. Talbot. 2007. Assessment of future change in intensity-duration-frequency (IDF) curves for Southern Quebec using the Canadian Regional Climate Model (CRCM). *Journal of Hydrology* 347: 197-210.
- Malanson, G. P. 1984. Intensity as a third factor of disturbance regime and its effect on species diversity. *Oikos* 43: 411-413.
- Marshall, N. A. and P. C. E. Bailey. 2004. Impact of secondary salinisation on freshwater ecosystems: effects of contrasting, experimental, short-term releases of saline wastewater on macroinvertebrates in a lowland stream. *Marine and Freshwater Research* 55: 509-523.

- Martens, D. W. and J. A. Servizi. 1993. Suspended sediment particles inside gills and spleens of juvenile pacific salmon (*Oncorhynchus* spp.). Canadian Journal of Fisheries and Aquatic Sciences 50: 586-590.
- Mastin, B. J. and J. J. H. Rodgers. 2000. Toxicity and bioavailability of copper herbicides (clearigate, cutrine-plus, and copper sulfate) to freshwater animals. Archives of Environmental Contamination and Toxicology 39: 445-451.
- Matthaei, C. D., F. Weller, D. W. Kelly, and C. R. Townsend. 2006. Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. Freshwater Biology 51: 2154-2172.
- Mauchly, J. W. 1940. Significance test for sphericity of a normal n -variate distribution. Annals of Mathematical Statistics 11: 204-209.
- McArdle, B. H., K. J. Gaston, and J. H. Lawton. 1990. Variation in the size of animal populations: patterns, problems and artefacts. The Journal of Animal Ecology 59: 439-454.
- McArdle, B. H. and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82: 290-297.
- McAuliffe, J. R. 1984a. Competition for space, disturbance, and the structure of a benthic stream community. Ecology 65: 894-908.
- McAuliffe, J. R. 1984b. Competition for space, disturbance, and the structure of a benthic stream community. Ecology 65: 894-908.
- McCabe, D. J. and N. J. Gotelli. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. Oecologia 124: :270–279.
- McCormick, P. V. and R. J. Stevenson. 1991. Mechanisms of benthic algal succession in lotic environments. Ecology 72: 1835-1848.
- McCormick, P. V., R. B. E. Shuford Iii, and M. J. Chimney. 2006. Periphyton as a potential phosphorus sink in the Everglades Nutrient Removal project. Ecological Engineering 27: 279-289.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21: 178-185.

- McIntyre, P. B., E. Michel, K. France, A. Rivers, P. Hakizimana, and A. S. Cohen. 2005. Individual- and assemblage-level effects of anthropogenic sedimentation on snails in Lake Tanganyika. *Conservation Biology* 19: 171-181.
- McLeay, D. J., I. K. Birtwell, G. F. Hartman, and G. L. Ennis. 1987. Responses of Artic grayling (*Thymallus arcticus*) to acute and prolonged exposure to Yukon placer mining sediment. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 658-673.
- Meffe, G. K. 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. *Ecology* 65: 1525-1534.
- Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: Variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64: 250-286.
- Merritt, R. W. and K. W. Cummins. 1996. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque, IA.
- Merritt, R. W. and K. W. Cummins. 2006. Trophic relationships of macroinvertebrates. Pages 585-611 in F. R. Hauer and G. A. Lamberti, editors. *Methods in Stream Ecology*. Academic Press, London.
- Meyer, B. S. and A. C. Heritage. 1941. Effect of turbidity and depth of immersion on apparent photosynthesis in *Ceratophyllum Demersum*. *Ecology* 22: 17-22.
- Micheli, F., K. L. Cottingham, J. Bascompte, O. N. Björnstad, G. L. Eckert, J. M. Fischer, T. H. Keitt, B. E. Kendall, J. L. Klug, and J. A. Rusak. 1999. The dual nature of community variability. *Oikos* 85: 161-169.
- Michener, W. K., E. R. Blood, K. L. Bildstein, M. M. Brinson, and L. R. Gardner. 1997. Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications* 7: 770-801.
- Miller, F. J., P. M. Schlosser, and D. B. Janszen. 2000. Haber's rule: a special case in a family of curves relating concentration and duration of exposure to a fixed level of response for a given endpoint. *Toxicology* 149: 21-34.
- Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. *The American Naturalist* 120: 533-536.

- Miner, J. G. and R. A. Stein. 1993. Interactive influence of turbidity and light on larval bluegill (*Lepomis macrochirus*) foraging. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 781-788.
- Mintzer, I. M. 1992. *Confronting Climate Change: Risks, Implications and Responses*. Cambridge University Press, Cambridge.
- Mol, J. H. and P. E. Ouboter. 2004. Downstream effects of erosion from small-scale gold mining on the instream habitat and fish community of a small neotropical rainforest stream. *Conservation Biology* 18: 201-214.
- Muller, R. A. and G. W. Stone. 2001. A climatology of tropical storm and hurricane strikes to enhance vulnerability prediction for the southeast U.S. Coast. *Journal of Coastal Research* 17: 949-956.
- Murphy, J. and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* 27: 31-36.
- Murray-Gulde, C. L., J. E. Heatley, A. L. Schwartzman, and J. J. H. Rodgers. 2002. Algicidal effectiveness of clearigate, cutrine-plus, and copper sulfate and margins of safety associated with their use. *Archives of Environmental Contamination and Toxicology* 43: 19-27.
- Musolff, A., S. Leschik, M. Möder, G. Strauch, F. Reinstorf, and M. Schirmer. 2009. Temporal and spatial patterns of micropollutants in urban receiving waters. *Environmental Pollution* 157: 3069-3077.
- Mutshinda, C. M., R. B. O'Hara, and I. P. Woiwod. 2009. What drives community dynamics? *Proceedings of the Royal Society of London B* 276: 2923-2929.
- Navarrete, S. A. 1996. Variable predation: effects of whelks on a mid-intertidal succesional community. *Ecological Monographs* 66: 301-321.
- Nelson, R. L., M. L. McHenry, and W. S. Platts. 1991. Mining. Pages 425-457 in W. R. Meehan, editor. *Influences of Forest and Rangeland Management*. American Fisheries Society Special Publication 19, Bethesda, Maryland.
- Newcombe, C. P. and D. D. McDonald. 1991. Effects of suspended sediments on aquatic ecosystems. *North American Journal of Fisheries Management* 11: 72-82.

- Newcombe, C. P. and J. O. T. Jensen. 1996. Channel suspended sediment and fisheries: a synthesis for quantitative assessment of risk and impact. *North American Journal of Fisheries Management* 16: 693-727.
- Newcombe, C. P. 2003. Impact assessment model for clear water fishes exposed to excessively cloudy water. *Journal of the American Water Resources Association* 39: 529-544.
- Norkko, A., R. Rosenberg, S. F. Thrush, and R. B. Whitlatch. 2006. Scale- and intensity-dependent disturbance determines the magnitude of opportunistic response. *Journal of Experimental Marine Biology and Ecology* 330: 195-207.
- Notestein, S. K., T. K. Frazer, M. V. Hoyer, and D. E. Canfield, Jr. 2003. Nutrient limitation of periphyton in a spring-fed, coastal stream in Florida, USA. *Journal of Aquatic Plant Management* 41: 57-60.
- Odum, E. P., J. T. Finn, and H. F. Eldon. 1979. Perturbation theory and the subsidy-stress gradient. *Bioscience* 29: 349-352.
- Odum, E. P. 1984. The mesocosm. *Bioscience* 34: 558-562.
- Omann, I., A. Stocker, and J. Jäger. 2009. Climate change as a threat to biodiversity: an application of the DPSIR approach. *Ecological Economics* 69: 24-31.
- Onderka, M. and P. Pekárová. 2008. Retrieval of suspended particulate matter concentrations in the Danube River from Landsat ETM data. *Science of the Total Environment* 397: 238-243.
- Ostrander, G. K., K. M. Armstrong, E. T. Knobbe, D. Gerace, and E. P. Scully. 2000. Rapid transition in the structure of a coral reef community: The effects of coral bleaching and physical disturbance. *Proceedings of the National Academy of Sciences of the United States of America* 97: 5297-5302.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1: 535-545.
- Palmer, M. A., C. C. Hakenkamp, and K. Nelson-Baker. 1997. Ecological heterogeneity in streams: why variance matters. *Journal of the North American Benthological Society* 16: 189-202.
- Pathikonda, S., A. S. Ackleh, K. H. Hasenstein, and S. Mopper. 2009. Invasion, disturbance, and competition: modeling the fate of coastal plant populations. *Conservation Biology* 23: 164-173.

- Pausas, J. G., R. A. Bradstock, D. A. Keith, and J. E. Keeley. 2004. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85: 1085-1100.
- Pearson, W. D. and D. R. Franklin. 1968a. Some factors affecting drift rates of *Baetis* and *Simuliidae* in a large river. *Ecology* 49: 75-81.
- Pearson, W. D. and D. R. Franklin. 1968b. Some factors affecting drift rates of *Baetis* and *Simuliidae* in a large river. *Ecology* 49: 75-81.
- Peeters, E., B. Brugmans, J. Beijer, and R. Franken. 2006. Effect of silt, water and periphyton quality on survival and growth of the mayfly *Heptagenia sulphurea*. *Aquatic Ecology* 40: 373-380.
- Pentz, S. B. and R. A. Kostaschuk. 1999. Effect of placer mining on suspended sediment in reaches of sensitive fish habitat. *Environmental Geology* 37: 78-89.
- Peterson, C. G. and R. J. Stevenson. 1992. Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology* 73: 1445-1461.
- Piazzzi, L., D. Balata, F. Cinelli, and L. Benedetti-Cecchi. 2004. Patterns of spatial variability in epiphytes of *Posidonia oceanica*: differences between a disturbed and two reference locations. *Aquatic Botany* 79: 345-356.
- Pickett, S. T. A. and P. S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, Florida.
- Pimentel, D., C. Harvey, P. Resosudarmo, K. Sinclair, D. Kurz, M. McNair, S. Crist, L. Shpritz, L. Fitton, R. Saffouri, and R. Blair. 1995. Environmental and economic costs of soil erosion and conservation benefits. *Science* 267: 1117-1123.
- Platt, W. J. and J. H. Connell. 2003. Natural disturbances and directional replacement of species. *Ecological Monographs* 73: 507-522.
- Poff, N. L. and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Science* 46: 1805-1818.
- Poff, N. L., B. P. Bledsoe, and C. O. Cuhacyan. 2006. Hydrologic variation with land use across the contiguous United States: Geomorphic and ecological consequences for stream ecosystems. *Geomorphology* 79: 264-285.

- Porter, E., T. Blett, D. U. Potter, and C. Huber. 2005. Protecting resources on federal lands: implications of critical loads for atmospheric deposition of nitrogen and sulfur. *Bioscience* 55: 603-611.
- Postel, S. L., G. C. Daily, and P. R. Ehrlich. 1996. Human appropriation of renewable fresh water. *Science* 271: 785-788.
- Potter, T. L., C. C. Truman, T. C. Strickland, D. D. Bosch, T. M. Webster, D. H. Franklin, and C. W. Bednarz. 2006. Combined effects of constant versus variable intensity simulated rainfall and reduced tillage management on cotton pre-emergence herbicide runoff. *Journal of Environmental Quality* 35: 1894-1902.
- Price, J. E., and P. J. Morin. 2004. Colonization history determines alternate community states in a food web of intraguild predators. *Ecology* 85: 1017-1028.
- Quinn, J. M., R. J. Davies-Colley, C. W. Hickey, M. L. Vickers, and P. A. Ryan. 1992. Effects of clay discharges on streams. 2. Benthic invertebrates. *Hydrobiologia* 248: 235-247.
- Quinn, J. M. and M. J. Stroud. 2002. Water quality and sediment and nutrient export from New Zealand highland catchments of contrasting land use. *New Zealand Journal of Marine and Freshwater Research* 36: 409-429.
- Quintana, X. D. 2002. Measuring the intensity of disturbance in zooplankton communities of Mediterranean salt marshes using multivariate analysis. *Journal of Plankton Research* 24: 255-265.
- Rabeni, C. F. and M. A. Smale. 1995. Effects of siltation on stream fishes and the potential mitigating role of the buffering riparian zone. *Hydrobiologia* 303: 211-219.
- Radwell, A. J. and A. V. Brown. 2006. Influence of fine sediments on meiofauna colonization densities in artificial stream channels. *Archiv für Hydrobiologie* 165: 63-75.
- Relyea, R. A. and N. Mills. 2001. Predator-induced stress makes the pesticide Carbaryl more deadly to gray treefrog tadpoles (*Hyla versicolor*). *Proceedings of the National Academy of Sciences of the United States of America* 98: 2491-2496.
- Reynolds, J. B., R. C. Simmons, and A. R. Burkholder. 1989. Effects of placer mining discharge on health and food of Arctic Grayling. *Water Resources Bulletin* 25: 625-635.

- Rhind, S. M. 2009. Anthropogenic pollutants: a threat to ecosystem sustainability? Philosophical Transactions of the Royal Society B 364: 3391-3401.
- Ricciardi, A. and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. Conservation Biology 13: 1220-1222.
- Richards, C., G. E. Host, and J. W. Arthur. 1993. Identification of predominant environmental factors structuring stream macroinvertebrate communities within a large agricultural catchment. Freshwater Biology 29: 285-294.
- Richardson, J., D. K. Rowe, and J. P. Smith. 2001. Effects of turbidity on the migration of juvenile banded kokopu (*Galaxias fasciatus*) in a natural stream. New Zealand Journal of Marine and Freshwater Research 35: 191-196.
- Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. Conservation Biology 10: 1163-1174.
- Robinson, J. V. and C. D. Sandgren. 1983. The effect of temporal environmental heterogeneity on community structure: a replicated experimental study. Oecologia 57: 98-102.
- Robinson, J. V. and M. A. Edgemon. 1988. An experimental evaluation of the effect of invasion history on community structure. Ecology 69: 1410-1417.
- Rodríguez, M. A. and W. M. Lewis, Jr. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. Ecological Monographs 67: 109-128.
- Rood, K. M. 1984. An Aerial Photograph Inventory of the Frequency and Yield of Mass Wasting on the Queen Charlotte Islands, British Columbia. Land Management Report 34. British Columbia Ministry of Forests, Victoria, British Columbia. (Available from: <http://www.for.gov.bc.ca/hfd/pubs/Docs/Mr/Lmr034.htm>).
- Root, T. L. and S. H. Schneider. 1995. Ecology and climate: research strategies and implications. Science 269: 334-341.
- Rosenberg, D. M. and A. P. Wiens. 1978. Effects of sediment addition on macrobenthic invertebrates in a northern Canadian river. Water Research 12: 753-763.
- Rosenberg, D. M. and V. H. Resh. 1993. Freshwater Biomonitoring and Benthic Macroinvertebrates. Chapman and Hall, New York, NY.

- Rowe, D. K. and T. L. Dean. 1998. Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. *New Zealand Journal of Marine and Freshwater Research* 32: 21-29.
- Roxburgh, S. H., K. Shea, and J. B. Wilson. 2004. The Intermediate Disturbance Hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85: 359-371.
- Rozman, K. K. 2000. The role of time in toxicology or Haber's $c \times t$ product. *Toxicology* 149: 35-42.
- Ruane, N. M., E. A. Huisman, and J. Komen. 2002. The influence of feeding history on the acute stress response of common carp (*Cyprinus carpio*). *Aquaculture* 210: 245-257.
- Ryan, P. A. 1991. Environmental effects of sediment on New Zealand streams: a review. *New Zealand Journal of Marine and Freshwater Research* 25: 207-221.
- Rykiel, E. J., Jr. 1985. Towards a definition of ecological disturbance. *Austral Ecology* 10: 361-365.
- Sabo, J. L. and D. M. Post. 2008. Quantifying periodic, stochastic, and catastrophic environmental variation. *Ecological Monographs* 78: 19-40.
- Sala, O. E., F. S. Chapin III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Biodiversity - global biodiversity scenarios for the year 2100. *Science* 287: 1770-1774.
- Salomons, W. 1995. Environmental impact of metals derived from mining activities: processes, predictions, prevention. *Journal of Geochemical Exploration* 52: 5-23.
- Saltz, D., D. I. Rubenstein, and G. C. White. 2006. The impact of increased environmental stochasticity due to climate change on the dynamics of Asiatic wild ass. *Conservation Biology* 20: 1402-1409.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *The American Naturalist* 102: 243-282.
- Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. *Bioscience* 52: 891.
- Schindler, D. W., R. E. Hecky, D. L. Findlay, M. P. Stainton, B. R. Parker, M. J. Paterson, K. G. Beaty, M. Lyng, and S. E. M. Kasian. 2008. Eutrophication of lakes cannot be controlled by

reducing nitrogen input: results of a 37-year whole-ecosystem experiment. *Proceedings of the National Academy of Sciences of the United States of America* 105: 11254-11258.

Schoener, T. W. 1986. Mechanistic approaches to community ecology: a new reductionism? *American Zoologist* 26: 81-106.

Schwilk, D. W. 2003. Flammability is a niche construction trait: canopy architecture affects fire intensity. *The American Naturalist* 162: 725-733.

Scinto, L. J. and K. R. Reddy. 2003. Biotic and abiotic uptake of phosphorus by periphyton in a subtropical freshwater wetland. *Aquatic Botany* 77: 203-222.

Scrimgeour, G. J., J. M. Culp, and F. J. Wrona. 1994. Feeding while avoiding predators: evidence for a size-specific trade-off by a lotic mayfly. *Journal of the North American Benthological Society* 13: 368-378.

Servizi, J. A. and D. W. Martens. 1991. Effect of temperature, season and fish size on acute lethality of suspended sediments to coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 48: 493-497.

Servizi, J. A. and D. W. Martens. 1992. Sublethal responses of coho salmon (*Oncorhynchus kisutch*) to suspended sediments. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1389-1395.

Servizi, J. A., and D.W. Martens. 1991. Effect of temperature, season, and fish size on acute lethality of suspended sediments to coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries Aquatic Science* 48: 493-497.

Shaw, E. A. and J. S. Richardson. 2001. Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) growth and survival. *Canadian Journal of Fisheries Aquatic Science* 58: 2213-2221.

Shea, K., S. H. Roxburgh, E. S. J. Rauschert, and L. Blaustein. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* 7: 491-508.

Shoup, D. E. and D. H. Wahl. 2009. The effects of turbidity on prey selection by piscivorous largemouth bass. *Transactions of the American Fisheries Society* 138: 1018-1027.

- Shure, D. J. and D. L. Phillips. 1987. Litter fall patterns within different-sized disturbance patches in a southern Appalachian mountain forest. *American Midland Naturalist* 118: 348-357.
- Sigler, J. W., T. C. Bjornn, and F. H. Everest. 1984. Effects of chronic turbidity on density and growth of steelheads and coho salmon. *Transactions of the American Fisheries Society* 113: 142-150.
- Sih, A., A. M. Bell, and J. L. Kerby. 2004. Two stressors are far deadlier than one. *Trends in Ecology and Evolution* 19: 274-276.
- Smail, J. K. 2002. Confronting a surfeit of people: reducing global human numbers to sustainable levels. *Environment, Development and Sustainability* 4: 21-50.
- Smith, C. R. and S. J. Brumsickle. 1989. The effects of patch size and substrate isolation on colonization modes and rates in an intertidal sediment. *Limnology and Oceanography* 34: 1263-1277.
- Smith, V. H. and D. W. Schindler. 2009. Eutrophication science: where do we go from here? *Trends in Ecology and Evolution* 24: 201-207.
- Sohngen, B. L. and R. W. Haynes. 1997. The potential for increasing carbon storage in United States unreserved timberlands by reducing forest fire frequency: an economic and ecological analysis. *Climatic Change* 35: 179-197.
- Sommer, U. 1995. An experimental test of the intermediate disturbance hypothesis using cultures of marine phytoplankton. *Limnology and Oceanography* 40: 1271-1277.
- Sommer, U. 2000. Benthic microalgal diversity enhanced by spatial heterogeneity of grazing. *Oecologia* 122: 284-287.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15: 353-391.
- Southwood, T. R. E. 1996. The Croonian Lecture, 1995: Natural communities: structure and dynamics. *Philosophical Transactions: Biological Sciences* 351: 1113-1129.
- Speidel, M., C. D.G. Harley, M. J. Wonham. 2001. Recovery of the brown alga *Fucus gardneri* following a range of removal intensities. *Aquatic Botany* 71: 273-280.
- Standing Committee of Analysts. 1983. The Determination of Chlorophyll-*a* in Aquatic Environments, 1980. Her Majesty's Stationery Office, London.

- Steffen, W., P. J. Crutzen, and J. R. McNeill. 2007. The Anthropocene: are humans now overwhelming the great forces of Nature? *AMBIO: A Journal of the Human Environment* 36: 614-621.
- Steinman, D., G. A. Lamberti, and P. R. Leavitt. 2006. Biomass and pigments of benthic algae. Pages 357-381 in F. R. Hauer and G. A. Lamberti, editors. *Methods in Stream Ecology*. Academic Press, London.
- Suchanek, T. H. 1981. The role of disturbance in the evolution of life history strategies in the intertidal mussels *Mytilus edulis* and *Mytilus californianus*. *Oecologia* 50: 143-152.
- Suding, K. N. and D. Goldberg. 2001. Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. *Ecology* 82: 2133-2149.
- Sugden, H., R. Panusch, M. Lenz, M. Wahl, and J. C. Thomason. 2007. Temporal variability of disturbances: is this important for diversity and structure of marine fouling assemblages? *Marine Ecology* 28: 368-376.
- Suren, A. M. and I. G. Jowett. 2001. Effects of deposited sediment on invertebrate drift: an experimental study. *New Zealand Journal of Marine and Freshwater Research* 35: 725-737.
- Suren, A. M. 2005. Effects of deposited sediment on patch selection by two grazing stream invertebrates. *Hydrobiologia* 549: 205-218.
- Sutherland, A. B., J. L. Meyer, and E. P. Gardiner. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshwater Biology* 47: 1791-1805.
- Sutherland, A. B. and J. L. Meyer. 2007. Effects of increased suspended sediment on growth rate and gill condition of two southern Appalachian minnows. *Environmental Biology of Fishes* 80: 389-403.
- Suttle, K. B., M. E. Power, J. M. Levine, and C. McNeely. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications* 14: 969-974.
- Svensson, R., M. Lindegarth, and H. Pavia. 2009. Equal rates of disturbance cause different patterns of diversity. *Ecology* 90: 496-505.
- Swanson, F. J. and C. T. Dyrness. 1975. Impact of clear-cutting and road construction on soil erosion by landslides in the western Cascade Range, Oregon. *Geology* 3: 393-396.

- Swanston, D. N. 1991. Natural processes. American Fisheries Society Special Publication 19: 139-179.
- Sweka, J. A. and K. J. Hartman. 2001. Influence of turbidity on brook trout reactive distance and foraging success. Transactions of the American Fisheries Society 130: 138-146.
- Sykora, J. L., M. Synak, and E. J. Smith. 1972. Effect of lime neutralized iron hydroxide suspensions on juvenile brook trout (*Salvelinus fontinalis*, Mitchill). Water Research 6: 935-950.
- Syphard, A., V. Radeloff, J. Keeley, T. Hawbaker, M. Clayton, S. Stewart, and R. Hammer. 2007. Human influence on California fire regimes. Ecological Applications 17: 1388-1402.
- Syphard, A. D., V. C. Radeloff, T. J. Hawbaker, and S. I. Stewart. 2009. Conservation threats due to human-caused increases in fire frequency in Mediterranean-climate ecosystems. Conservation Biology 23: 758-769.
- Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. Ferreira de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. Nature 427: 145-148.
- Tilman, D. and C. Lehman. 2001. Human-caused environmental change: impacts on plant diversity and evolution. Proceedings of the National Academic of Sciences of the United States of America 98: 5433-5440.
- Townsend, C. R., M. R. Scarsbrook, and S. Doledec. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. Limnology and Oceanography 42: 938-949.
- Townsend, C. R., S. S. Uhlmann, and C. D. Matthaei. 2008. Individual and combined responses of stream ecosystems to multiple stressors. Journal of Applied Ecology 45: 1810-1819.
- Turnpenny, A. W. H. and R. Williams. 1980. Effects of sedimentation on the gravels of an industrial river system. Journal of Fish Biology 17: 681-693.
- U.S. EPA. 1991. Technical Support Document for Water Quality-Based Toxic Control. Office of Water, U.S. Environmental Protection Agency, Washington, DC.
- Underwood, A. J. 1989. The analysis of stress in natural populations. Biological Journal of the Linnean Society 37: 51-78.

- Underwood, A. J. 1997. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge.
- Underwood, A. J. and M. G. Chapman. 2000. Variation in abundances of intertidal populations: consequences of extremities of environment. *Hydrobiologia* 426: 25-36.
- Utne, A. C. W. 1997. The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore *Gobiusculus flavescens*. *Journal of Fish Biology* 50: 926-938.
- van der Maarel, E. 1993. Some remarks on disturbance and its relations to diversity and stability. *Journal of Vegetation Science* 4: 733-736.
- Van Nieuwenhuysse, E. E. and J. D. LaPerriere. 1986. Effects of placer gold mining on primary production in subarctic streams of Alaska. *Journal of the American Water Resources Association* 22: 91-99.
- Vasconcelos, M. d. C. and A. S. Melo. 2008. An experimental test of the effects of inorganic sediment addition on benthic macroinvertebrates of a subtropical stream. *Hydrobiologia* 610: 321-329.
- Verardo, D. J., P. N. Froelich, and A. McIntyre. 1990. Determination of organic carbon and nitrogen in marine sediments using the Carlo Erba NA-1500 analyzer. *Deep Sea Research Part A. Oceanographic Research Papers* 37: 157-165.
- Villarini, G., F. Serinaldi, J. A. Smith, and W. F. Krajewski. 2009. On the stationarity of annual flood peaks in the continental United States during the 20th century. *Water Resources Research* 45: 8.
- Vinebrooke, R. D., K. L. Cottingham, J. Norberg, M. Scheffer, S. I. Dodson, S. C. Maberly, and U. Sommer. 2004. Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. *Oikos* 104: 451-457.
- Vinyard, G. L. and W. J. O'Brien. 1976. Effects of light and turbidity on the reaction distance of bluegill (*Lepomis macrochirus*). *Journal of the Fisheries Research Board of Canada* 33: 2845-2849.
- Vitousek, P. M. 1994. Beyond global warming: Ecology and global change. *Ecology* 75: 1862-1876.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277: 494-499.

- Vörösmarty, C. J. and D. Sahagian. 2000. Anthropogenic disturbance of the terrestrial water cycle. *Bioscience* 50: 753-765.
- Vuori, K.-M. and I. Joensuu. 1996. Impact of forest drainage on the macroinvertebrates of a small boreal headwater stream: Do buffer zones protect lotic biodiversity? *Biological Conservation* 77: 87-95.
- Walker, L. R. and M. R. Willing. 1999. An introduction to terrestrial disturbances. Pages 1-17 in L. R. Walker, editor. *Ecosystems of Disturbed Ground*. Elsevier Science, Amsterdam.
- Wallen, I. E. 1951. The direct effect of turbidity on fishes. *Oklahoma Agricultural and Mechanical College Bulletin, Biological Series* 2 48: 1-27.
- Walters, D. M., D. S. Leigh, and A. B. Bearden. 2003. Urbanization, sedimentation, and the homogenization of fish assemblages in the Etowah River Basin, USA. *Hydrobiologia* 494: 5-10.
- Waters, T. F. 1995. *Sediment in Streams: Sources, Biological Effects and Control*. American Fisheries Society Monograph, Bethesda, Maryland.
- Webster, P. J., G. J. Holland, J. A. Curry, and H. R. Chang. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 309: 1844-1846.
- Wei, X., J. P. Kimmins, and G. Zhou. 2003. Disturbances and the sustainability of long-term site productivity in lodgepole pine forests in the central interior of British Columbia - an ecosystem modeling approach. *Ecological Modelling* 164: 239-256.
- Weller, E., N. Long, A. Smith, P. Williams, S. Ravi, J. Gill, R. Hennessey, W. Skornik, J. Brain, C. Kimmel, G. Kimmel, L. Holmes, and L. Ryan. 1999. Dose-rate effects of ethylene oxide exposure on developmental toxicity. *Toxicological Sciences* 50: 259-270.
- Wellnitz, T. and N. L. Poff. 2006. Herbivory, current velocity and algal regrowth: how does periphyton grow when the grazers have gone? *Freshwater Biology* 51: 2114-2123.
- Wernberg, T. and S. D. Connell. 2008. Physical disturbance and subtidal habitat structure on open rocky coasts: effects of wave exposure, extent and intensity. *Journal of Sea Research* 59: 237-248.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* 45: 229-299.

- White, P. S. and S. P. Bratton. 1980. After preservation: philosophical and practical problems of change. *Biological Conservation* 18: 241-255.
- White, P. S., J. Harrod, W. Romme, and J. Betancourt. 1999. The role of disturbance and temporal dynamics. Pages 281-312 in R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. *Ecological Stewardship*. Elsevier Science, Oxford.
- White, P. S. and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* 62: 399-449.
- Whitlatch, R. B., A. H. Hines, S. F. Thrush, J. E. Hewitt, and V. Cummings. 1997. Benthic faunal responses to variations in patch density and patch size of a suspension-feeding bivalve. *Journal of Experimental Marine Biology and Ecology* 216: 171-189.
- Wilbanks, T. J. and R. W. Kates. 1999. Global change in local places: how scale matters. *Climatic Change* 43: 601-628.
- Wilber, C. G. 1983. *Turbidity in the Aquatic Environment. An Environmental Factor in Fresh and Oceanic Waters*. Charles C. Thomas, Springfield, Illinois.
- Wilcove, D. S., D. Rothstein, D. Jason, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48: 607-615.
- Williams, D. D. and H. B. N. Hynes. 1976. The recolonization mechanisms of stream benthos. *Oikos* 27: 265-272.
- Wilson, J. B. 1990. Mechanisms of species coexistence: twelve explanations for Hutchinson's 'paradox of the plankton': evidence from New Zealand plant communities. *New Zealand Journal of Ecology* 13: 17-42.
- Wilson, K. P., J. P. Shannon, and D. W. Blinn. 1999. Effects of suspended sediment on biomass and cell morphology of *Cladophora glomerata* (chlorophyta) in the Colorado River, Arizona. *Journal of Phycology* 35: 36-41.
- Wilson, S. D. and D. Tilman. 2002. Quadratic variation in old-field species richness along gradients of disturbance and nitrogen. *Ecology* 83: 492-504.
- Wohl, E. 2006. Human impacts to mountain streams. *Geomorphology* 79: 217-248.

- Wollgast, S., M. Lenz, M. Wahl, and M. Molis. 2008. Effects of regular and irregular temporal patterns of disturbance on biomass accrual and species composition of a subtidal hard-bottom assemblage. *Helgoland Marine Research* 62: 309-319.
- Wood, P. J. and P. D. Armitage. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* 21: 203-217.
- Wood, P. J. and P. D. Armitage. 1999. Sediment deposition in a small lowland stream - management implications. *Regulated Rivers: Research & Management* 15: 199-210.
- Wu, J. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *The Quarterly Review of Biology* 70: 439-466.
- Wulff, A., K. Sundbäck, C. Nilsson, L. Carlson, and B. Jönsson. 1997. Effect of sediment load on the microbenthic community of a shallow-water sandy sediment. *Estuaries* 20: 547-558.
- Yamada, H. and F. Nakamura. 2002. Effect of fine sediment deposition and channel works on periphyton biomass in the Makomanai River, northern Japan. *Rivers Research and Applications* 18: 481-493.
- Yin, H. and C. Li. 2001. Human impact on floods and flood disasters on the Yangtze River. *Geomorphology* 41: 105-109.
- Yoshida, K. 2006. Effect of the intensity of stochastic disturbance on temporal diversity patterns: a simulation study in evolutionary time scale. *Ecological Modelling* 196: 103-115.
- Yuan, L. L. 2010. Estimating the effects of excess nutrients on stream invertebrates from observational data. *Ecological Applications* 20: 110-125.
- Zhang, D. D., P. Brecke, H. F. Lee, Y. Y. He, and J. Zhang. 2007. Global climate change, war, and population decline in recent human history. *Proceedings of the National Academic of Sciences of the United States of America* 104: 19214-19219.
- Zhang, X. C., L. D. Norton, and M. Hickman. 1997. Rain pattern and soil moisture content effects on atrazine and metolachlor losses in runoff. *Journal of Environmental Quality* 26: 1539-1547.
- Zhibin, Z., X. I. E. Yan, and W. U. Yuming. 2006. Human disturbance, climate and biodiversity determine biological invasion at a regional scale. *Integrative Zoology* 1: 130-138.

- Zweig, L. D. and C. F. Rabeni. 2001. Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. *Journal of the North American Benthological Society* 20: 643-657.

Appendices



Massive earth slump resulting from intense river bank erosion
(photo by U.S. Department of Agriculture)

Appendix A. List of macroinvertebrate taxa and respective functional feeding groups (FFG) identified in drift and benthic samples during the experiment presented in Chapter III.

Taxa	FFG	Immediate drift	Delayed drift	Benthos <i>in situ</i>
PLECOPTERA				
<i>Siphonoperla torrentium</i> (Pictet)	P	+	+	+
<i>Protonemura meyeri</i> (Pictet)	SH	+	+	+
<i>Amphinemura sulcicollis</i> (Stephens)	SH	+	+	+
<i>Leuctra inermis</i> (Kempny)	SH	+	+	+
<i>Leuctra hippopus</i> (Kempny)	SH	+	+	+
<i>Leuctra</i> sp.	SH	+		+
<i>Isoperla grammatica</i> (Poda)	P	+	+	+
TRICHOPTERA				
Limnephilidae (early instar)	SH	+	+	+
<i>Chaetopteryx villosa</i> (Fabricius)	SH	+	+	+
<i>Drusus annulatus</i> (Stephens)	SH	+	+	+
<i>Potamophylax cingulatus</i> (Stephens)	SH			+
<i>Rhyacophila dorsalis</i> (Curtis)	P	+	+	+
<i>Rhyacophila munda</i> (McLachlan)	P	+	+	+
<i>Tinodes waeneri</i> (Linnaeus)	CG			+
<i>Lepidostoma hirtum</i> (Fabricius)	SH	+	+	+
<i>Polycentropus kingi</i> (McLachlan)	P	+	+	+
<i>Plectrocnemia geniculata</i> (McLachlan)	P		+	+
<i>Plectrocnemia conspersa</i> (Curtis)	P	+	+	+
EPHEMEROPTERA				
<i>Baetis rhodani</i> (Pictet)	CG		+	+
<i>Siphonurus lacustris</i> (Eaton)	CG	+	+	+
DIPTERA				
<i>Dicranota</i> sp.	SH	+		+
Empididae	P			+
Simuliidae	CF	+	+	+
Chironomidae	CG	+	+	+

Note: SH: shredder; CG: collector-gatherer; CF: collector -filterer; P: predator; S: scraper

Appendix A. Continued.

Taxa	FFG	Immediate drift	Delayed drift	Berthos
COLEOPTERA				
<i>Limnius volckmari</i> (Panzer)	S	+	+	+
<i>Limnius volckmari</i> (Panzer) (larva)	S			+
<i>Elmis aena</i> (Müller) (larva)	S			+
<i>Oulimnius tuberculatus</i> (Müller)	S		+	+
<i>Oulimnius tuberculatus</i> (Müller) (larva)	S			+
<i>Esolus parallelepipedus</i> (Müller)	S	+	+	+
<i>Esolus parallelepipedus</i> (Müller) (larva)	S			+
<i>Hyphydrus ovatus</i> (Linnaeus)	P		+	+
<i>Oreodytes sanmarkii</i> (Sahlberg)	P		+	+
<i>Oreodytes septentrionalis</i> (Gylenhall)	P		+	+
<i>Plateumaris</i> sp.	SH	+		+
<i>Gyrinus urinator</i> (Illiger)	P		+	+
GASTROPODA				
<i>Anacaena globulus</i> (Paykull)	S	+	+	+
<i>Planorbis carinatus</i> (Müller)	S		+	+
<i>Limnaea</i> sp.	S	+		+
HEMIPTERA				
<i>Hebrus ruficeps</i> (Thomson)	P		+	
<i>Gerris</i> sp.	P		+	+
<i>Microvelia</i> sp.	P	+		
<i>Sigara venusta</i> (Douglas & Scott)	S		+	+
COLLEMBOLA	CG	+	+	+
OLIGOCHAETA	CG			+
TURBELLARIA	CG			+
ACARI				
Hydracarina	P		+	+

Note: SH: shredder; CG: collector-gatherer; CF: collector-filterer; P: predator; S: scraper

Appendix B. List of macroinvertebrate taxa and corresponding functional feeding groups found in benthic samples during the experiment presented in Chapter IV.

Taxon	Functional feeding group
PLECOPTERA	
<i>Brachyptera risi</i> (Morton)	Scraper
<i>Chloroperla tripunctata</i> (Scopoli)	Predator
<i>Protonemura meyeri</i> (Pictet)	Shredder
<i>Amphinemura sulcicollis</i> (Stephens)	Shredder
<i>Leuctra</i> sp.	Shredder
<i>Isoperla grammatica</i> (Poda)	Predator
TRICHOPTERA	
<i>Chaetopteryx villosa</i> (Fabricius)	Shredder
<i>Glossosoma boltoni</i> (Curtis)	Scraper
<i>Hydropsyche siltalai</i> (Döhler)	Collector filterer
<i>Odontocerum albicorne</i> (Scopoli)	Shredder
<i>Rhyacophila dorsalis</i> (Curtis)	Predator
<i>Rhyacophila munda</i> (McLachlan)	Predator
<i>Sericostoma personatum</i> (Kirby & Spence)	Shredder
<i>Lepidostoma hirtum</i> (Fabricius)	Shredder
<i>Polycentropus kingi</i> (McLachlan)	Predator
<i>Silo nigricornis</i> (Pictet)	Scraper
<i>Plectrocnemia conspersa</i> (Curtis)	Predator
EPHEMEROPTERA	
<i>Baetis rhodani</i> (Pictet)	Collector gatherer
<i>Caenis rivulorum</i> (Eaton)	Collector gatherer
<i>Ephemerella ignita</i> (Poda)	Collector gatherer
<i>Rhithrogena semicolorata</i> (Curtis)	Scraper
DIPTERA	
<i>Ceratopogonidae</i>	Predator
<i>Dicranota</i> sp.	Predator
<i>Empididae</i>	Predator
<i>Chelifera</i> sp.	Predator
<i>Chironomidae</i>	Collector gatherer
<i>Psychodidae</i>	Collector gatherer

Appendix B. Continued.

Taxon	Functional feeding group
<i>Simuliidae</i>	Collector filterer
COLEOPTERA	
<i>Elmis aena</i> (Müller) (larva)	Scraper
<i>Esolus parallelepipedus</i> (Müller)	Scraper
<i>Esolus parallelepipedus</i> (Müller) (larva)	Scraper
<i>Gyrinus</i> sp. (larva)	Predator
<i>Elodes</i> sp. (larva)	Scraper
<i>Hydraena gracilis</i> (Germar)	Scraper
<i>Hydrocyphon deflexicollis</i> (Müller) (larva)	Scraper
<i>Limnius volckmari</i> (Panzer)	Scraper
<i>Limnius volckmari</i> (Panzer) (larva)	Scraper
<i>Stictonectes Lepidus</i> (Olivier)	Piercer
GASTROPODA	
<i>Ancylus fluviatilis</i> (Müller)	Scraper
BIVALVA	
<i>Pisidium</i> sp.	Collector filterer
AMPHIPODA	
<i>Gammarus duebeni</i> (Liljeborg)	Collector gatherer
NEMATODA	Parasite
ACARI	
<i>Leberetia</i> sp.	Predator
<i>Sperchon</i> sp.	Predator
OLIGOCHAETA	Collector gatherer
TURBELLARIA	Collector gatherer