

Temporal variability within disturbance events regulates their effects on natural communities

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Abstract Disturbances are processes inherently variable in time and space. This variability comprises a key determinant of ecosystem responses to disturbance. Temporal patterns can, however, vary significantly both among and within individual disturbance events. While recent research has demonstrated an importance of the former, studies on the effects of variability within perturbations have consistently confounded temporal variability with other disturbance attributes (e.g. overall intensity or duration). We established a field experiment to test explicitly the hypothesis that the temporal pattern within perturbations can drive ecosystem responses independently of other disturbance traits. We examined the effects of two disturbance regimes comprising sediment pulses of contrasting temporal pattern (constant and temporally variable intensities) on the benthic invertebrate assemblage of a headwater stream. The overall intensity, duration, timing and frequency of the perturbations were, however, identical. Invertebrates drifting during the temporally variable pulses were more abundant and differed in taxonomic and trophic structure than those exposed to constant perturbations. Moreover, whereas temporal patterns of disturbance events had no immediate effect on benthic invertebrate assemblages in situ, assemblages exposed to the constant perturbations took longer to recover from sediment disturbances than those exposed to temporally variable perturbations. Our results demonstrate that variability in the temporal pattern of intensity within

individual perturbations can regulate, independently of other disturbance attributes, the extent and type of ecosystem responses to, and recovery from, disturbances. Effective environmental management and policy therefore necessitate the explicit quantification of temporal patterns of intensity both within and among perturbations.

Keywords Disturbance · Community · Sediment · Stream macroinvertebrates · Temporal pattern

Introduction

Disturbances are a major source of temporal and spatial heterogeneity in natural communities and constitute a key driver of natural selection (Roxburgh et al. 2004; Fraterrigo and Rusak 2008; Pathikonda et al. 2009). 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 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; Zhang et al. 2007). Understanding and planning for the ecological impacts of disturbances constitute, therefore, an urgent necessity for scientists, managers and policy-makers alike (Lubchenco 1998).

One of the greatest challenges for the study of disturbances is the degree of temporal variability inherent both within and among individual perturbation events (Pickett and White 1985; White and Jentsch 2001; Benedetti-Cecchi 2003; García Molinos and Donohue 2010). Different attributes of disturbances, including their frequency (McCabe

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and Gotelli 2000) and duration (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 into two components: heterogeneity in the distribution of perturbations over time (i.e. among perturbations; Benedetti-Cecchi 2000, 2003; García Molinos and Donohue 2010) and that embodied within individual perturbation events. With the exception of some early studies (e.g. Robinson and Sandgren 1983), experimentation into the effects of temporal variability among perturbations has traditionally been approached by varying 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 unit 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 variability of disturbance processes, which has led to further research into the subject (Bertocci et al. 2005; Benedetti-Cecchi et al. 2006; Atalah et al. 2007).

Characterisation of the temporal pattern within individual perturbations in experimental disturbance ecology has focussed traditionally on disturbance duration (Bender et al. 1984; Glasby and Underwood 1996), typically involving a contrast of prolonged (pressed) versus discrete (pulse) perturbations (e.g. Marshall and Bailey 2004). However, such 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 (Schwilk 2003; Crosa et al. 2010). Both theoretical (Lake 2000) and empirical (Sabo and Post 2008) studies have recognised the importance of temporal variability in intensity within perturbations. However, the few experimental studies that have investigated its ecological implications tend to compare the effects of gradual versus abrupt pressed (e.g. Klironomos et al. 2005) or pulsed (e.g. Imbert and Perry 2000) changes. These studies indicated 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. However, these experiments consistently confounded the effects of temporal variability in intensity 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, the flow increases differed in duration. Similarly, Irvine and Henriques (1984) set flood pulses to be of equal duration, but differences in the rate of change made the intensity differ by

several orders of magnitude among treatments. 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 remain the same. Such variability is known to alter environmental conditions by modifying, for example, pollutant availability (Potter et al. 2006).

Quantification of the effects of varying temporal patterns of intensity within perturbation events, independent of other disturbance traits, is essential to attain a mechanistic understanding of the effects of the temporal pattern of disturbances on ecosystems and, thus, for effective management. To address this, we established a field experiment in which the benthic invertebrate assemblages in a headwater stream were exposed to two sediment disturbance regimes differing solely in the temporal pattern of intensity within their constituent perturbations (i.e. comprising a succession of identical sediment pulses of either constant or temporally variable intensity; Fig. 1). To unconfound the effects of temporal variability within perturbations from those of other disturbance traits, the frequency (number of perturbations per unit time), overall intensity (strength of disturbances), duration and process stochasticity (time elapsing between consecutive disturbances) of perturbations were equal across all disturbed treatments.

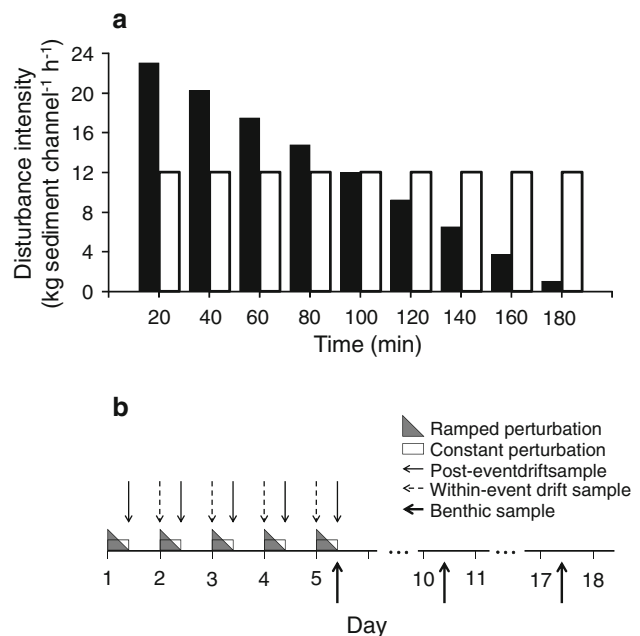


Fig. 1 **a** Volumes of sediment added to the experimentally disturbed channels during 5 days of constant (*open bars*) and variable (*closed bars*) perturbation events. **b** Schematic representation of the distribution of constant (*pressed*) versus variable (*ramped*) sediment pulses and the timing of sampling events during the experiment. Both treatments comprised disturbances of the same mean intensity and duration

Methods

Experimental design

We established our field experiment in a uniform riffle reach of the River Liffey (County Wicklow, Ireland; latitude 53°09.72'N, longitude 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 experimental site had little riparian canopy and was characterised by relatively uniform bed morphology dominated by gravel, cobbles and boulders.

We 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. Increased sediment loading comprises one of the most important and pervasive anthropogenic disturbances of aquatic ecosystems globally (Wood and Armitage 1997; Donohue and García Molinos 2009). 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 (*sensu* Lake 2000), with dosage decreasing consistently over the total length of the disturbances (variable treatment) (Fig. 1). Ramped pulses are common in sediment disturbances resulting from anthropogenic activities, such as effluent discharge and extractive operations (Krishnaswamy et al. 2006; Banas et al. 2008; Gomi et al. 2010). Both regimes were applied over 5 days and had otherwise constant frequency (1 perturbation every 21 h) and comprised disturbances of the same mean intensity ($12 \text{ kg soil h}^{-1}$) and duration (3 h) (Fig. 1). Our experimental treatments were complemented by procedural controls (undisturbed channels) and a control reach outside the channels located in a structurally similar riffle located 30 m upstream from the experimental site. These control treatments enabled the quantification of both concurrent natural patterns and processes at the experimental site in addition to any potential effects of our undisturbed experimental channels. Allocation of treatments to the experimental units was done randomly with three replications per treatment.

Nine bottomless channels (2.5 m long \times 0.4 m wide \times 1.0 m high), ballasted with boulders, were placed adjacent to each other across the experimental site and parallel to the direction of flow. Care was taken to avoid disturbance of the stream bed. Channels retained similar hydraulic conditions over the 5 days of experimental sediment disturbances, with a mean [± 1 standard deviation (SD), $n = 45$] water depth of $0.27 \pm 0.05 \text{ m}$ and velocity [taken at 0.4-fold the depth above the stream bed with a Sensa-RC2 electromagnetic

flow meter (Aqua Data Services, Wiltshire, UK)] of $0.29 \pm 0.05 \text{ m s}^{-1}$. Sieved ($< 2 \text{ mm}$) top soil was combined with stream water in circular 450-L tanks and supplied to the channels by gravity, following the predefined temporal patterns for each treatment (Fig. 1a), 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 analyser; Malvern Instruments, Worcestershire, UK) of the sediment (± 1 SD, $n = 10$) supplied to the channels was $62 \pm 21.8\%$ silt and clay ($< 63 \mu\text{m}$), $19.2 \pm 12.2\%$ fine sand ($63 \mu\text{m}$ to 0.125 mm), $15.7 \pm 10.5\%$ medium sand ($0.125\text{--}0.5 \text{ mm}$) and $2.2 \pm 0.9\%$ coarse sand ($0.5\text{--}2 \text{ mm}$). Organic matter content of the sediment, determined by loss on ignition (24 h at 60°C followed by 3 h at 550°C), was $3.3 \pm 0.4\%$. 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 (Fig. 1b).

Sampling and laboratory analyses

Water turbidity was quantified (2100P HACH turbidimeter; HACH, Loveland, Colorado, USA) from the middle section of each channel every 20 min during the disturbances. Water samples were also taken from the same location to quantify total suspended solids 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 $< 4^\circ\text{C}$ and returned to the laboratory for analysis following standard methods (Clesceri et al. 1999). Sediment traps (0.12 m long \times 0.22 m wide) were embedded in the stream bed, flush with the bed surface, at the transversal mid-point of 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 ($< 2 \text{ mm}$) mass.

Nets (0.4 \times 0.4 m, 500- μm mesh) were attached to the outlet of each channel to quantify invertebrate drift. The dimensions and mesh size of the nets were sufficient to ensure the throughput of all of the water flowing through the experimental channels. We did not attempt to block any invertebrate drift from upstream of our experimental channels because temporal variability in background rates of invertebrate drift, including that from upstream of the experimental channels, was accounted for by our experimental design. Moreover, invertebrate drift distances have

been shown in general to be lower than 2 m at velocities similar to those encountered in our 2.5-m long experimental channels (e.g. Elliot 2002; Gibbins et al. 2007a). Drift was measured both before and after sediment addition over the 5 days of experimental disturbance to account for possible direct (within-event drift; occurring during each 3-h disturbance) and indirect (post-event drift; integrated over the 21 h between consecutive disturbances) responses to our experimental treatments. Our attempts at placing drift nets at the upstream control site failed owing to the unstable nature of the stream bed. To standardise the number of animals drifting by the volume of water flowing through the nets per unit of time, drift values were calculated as drift densities (number of individuals per 100 m³ of water). 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. 1b). 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 (diameter 0.30 m, mesh size 250 µm). 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 following Merritt and Cummins (1996).

Data analyses

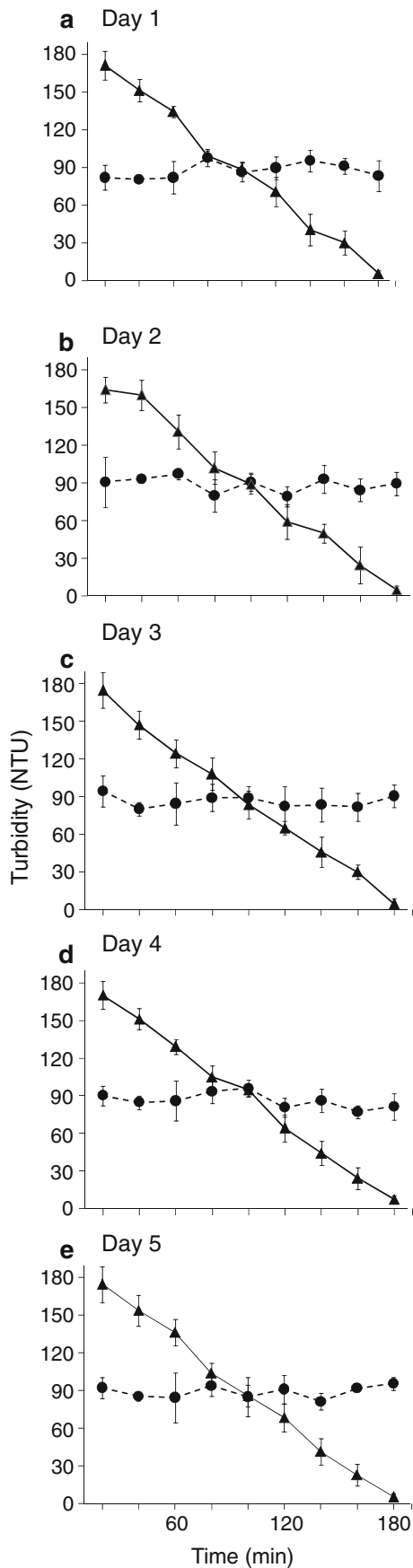
The effects of varying temporal patterns within perturbations on the abundance and taxon richness of invertebrate drift and benthic assemblages in situ were analysed with repeated measures analysis of variance (ANOVA) with SPSS ver. 15.0 (Apache Software Foundation, SPSS, Chicago, IL). The experimental treatment comprised the among-subjects fixed factor with four levels for in situ benthos (i.e. constant, variable, procedural control and upstream control treatments) and three levels for drift (no upstream control treatment). Sampling day provided repeated measures on treatment with five, four and three levels for within-event drift, post-event drift and in situ benthos, respectively (Fig. 1b). 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 (Hurlbert 1971). Rarefied

species richness was then analysed as the dependent variable in the ANOVA. Owing to the consistently small size of within-event drift samples from the procedural control channels (minimum sample size of two), rarefaction of within-event drift was performed only on samples from the disturbed channels. Checks for normality and homogeneity of variance (Levene 1960) were performed on all data, and transformations applied when necessary. Values for dependent variables are reported throughout as the mean \pm 1 SD.

We used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; McArdle and Anderson 2001) based on Bray–Curtis (Bray and Curtis 1957) similarity matrices calculated from $\log(x + 1)$ -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 9,999 permutations of the residuals under a reduced model. Abundance data were transformed prior to the calculation of the similarity among samples to down-weight the relative contribution of some numerically dominant species (Clarke and Warwick 2001). 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. We used an arbitrary percent dissimilarity contribution threshold of 3% to highlight only those taxa that contributed most to compositional differences among treatments. All multivariate analyses were performed using PRIMER ver. 6.1.8 (PRIMER-E Ltd, Plymouth, UK) with the PERMANOVA+ add-in (vers. 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. 2). Suspended solid concentrations during sediment pulses were 184.8 ± 20 mg L⁻¹ for the constant treatment and ranged from 331.1 ± 23.3 to 27.4 ± 6.9 mg L⁻¹ for the variable treatment. Concentrations of suspended solids in the control channels were 1.1 ± 0.6 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 ± 6.2 mg cm⁻² day⁻¹) did not, however, differ from each other but were significantly higher than background stream levels (0.5 ± 0.2 mg cm⁻² day⁻¹; $p < 0.001$ in both cases).



◀ **Fig. 2** a–e Daily turbidities [mean ± standard deviation (SD), $n = 3$] for each of the constant (filled circle with dashed line) and variable (filled triangle with solid line) sediment pulses comprising the two experimental disturbance treatments. Background water turbidity over the duration of the experiment was 0.77 ± 0.30 nephelometric turbidity units (NTU) ($n = 15$)

Invertebrate drift

The temporal pattern within sediment perturbations produced significant differences in the density (Table 1), assemblage composition and trophic characteristics (Table 2) of invertebrates drifting from the experimental channels during the addition of sediment (within-event drift; Fig. 3a). Each treatment differed significantly ($p < 0.01$) from every other for each response variable. The highest within-event drift densities corresponded to the variable treatment and the lowest to the control channels, of which the latter registered very low densities comprising almost exclusively plecopteran shredders. Chironomids, simuliids and a number of plecopteran taxa consistently contributed the most to pairwise differences in the composition of drift between treatments (Table 3). No difference was, however, found in rarefied taxon richness of within-event drift between the constant and the variable disturbance treatments (Table 1; Fig. 3c).

Experimental treatment and time interacted significantly in their effects on the densities of invertebrates drifting among disturbances (post-event drift; Table 1). Drift densities were significantly higher from disturbed (constant and variable) channels than from control channels on every day ($p < 0.05$), with no difference found between the two disturbed treatments (Fig. 3b). The number of invertebrates drifting among disturbances from channels under both disturbance treatments increased significantly over the duration of the experiment; post-event drift in both disturbance treatments was significantly higher at the end of the disturbance regime (Day 4) than during the first 2 days of the experiment ($p < 0.05$). The temporal patterning of sediment disturbances also produced significant differences in the rarefied taxon richness of the post-event drift (Table 1; Fig. 3d). Richness from the constant disturbance treatment was significantly higher than that from the variable treatment ($p < 0.01$). Post-event drift from neither treatment differed significantly in terms of rarefied taxon richness to that from the procedural controls; however, the difference between the constant disturbance treatment and the procedural control bordered on statistical significance ($p = 0.065$).

The taxonomic composition and trophic structure of post-event drift varied significantly among the experimental treatments (Table 2). The treatment effect corresponded to a difference between the disturbed and undisturbed

Table 1 Results of the analysis of variance (ANOVA) examining the effects of the sediment disturbance pattern on the density and rarefied taxon richness of invertebrate drift and benthic assemblages in situ

Source of variation	Transformation	df	Density			Taxon richness		
			MS	F	p	MS	F	p
Within-event drift	Log (1 + x)							
Between subjects								
Treatment		2	2.46	505.26	<0.001	0.01	0.01	0.95
Error		6	0.005			1.8		
Within subjects								
Day		4	0.009	0.67	0.62	2.5	1.9	0.17
Day × treatment		8	0.006	0.44	0.88	1.3	1	0.43
Error		24	0.013			1.3		
Post-event drift	None							
Between subjects								
Treatment		2	19.94	47.6	<0.001	4.7	11.6	0.009
Error		6	0.42			0.4		
Within subjects								
Day		3	2.85	9.3	0.001	0.9	0.46	0.72
Day × treatment		6	1.02	3.35	0.022	1.9	1.03	0.44
Error		18	0.31			1.9		
Macroinvertebrate benthos in situ	None							
Between subjects								
Treatment		3	5,127.3	19.3	0.001	35.5	14.4	0.001
Error		8	266.1			2.5		
Within subjects								
Day		2	8,804.3	44.7	<0.001	11.9	5.9	0.012
Day × treatment		6	2,758	14	<0.001	0.5	0.25	0.96
Error		16	197.1			2		

Table 2 Results of the permutational multivariate analysis of variance (PERMANOVA) examining the effects of the sediment disturbance pattern on the assemblage composition and trophic structure of invertebrate drift and benthic assemblages in situ

Source of variation	df	Assemblage composition			Trophic structure		
		MS	Pseudo-F	p	MS	Pseudo-F	p
Within-event drift							
Treatment	2	18,583	20.3	0.001	21,940	93	<0.001
Day	4	1,207	1.1	0.31	224.51	0.5	0.94
Day × treatment	8	914.27	0.9	0.76	235.98	0.5	0.98
Error	30	1,070.7			444.96		
Post-event drift							
Treatment	2	1,901.4	4.9	0.005	803.07	9	0.007
Day	3	538.14	1.3	0.15	181.69	1.9	0.079
Day × treatment	6	385.6	1	0.57	89.1	0.9	0.55
Error	24	405.72			98.07		
Macroinvertebrate benthos							
Treatment	3	1,478.7	5.1	0.007	177.2	4.1	0.049
Day	2	752.5	3	<0.001	151.8	20.4	<0.001
Day × treatment	6	289.2	1.2	0.19	42.8	5.8	<0.001
Error	24	250.2			7.4		

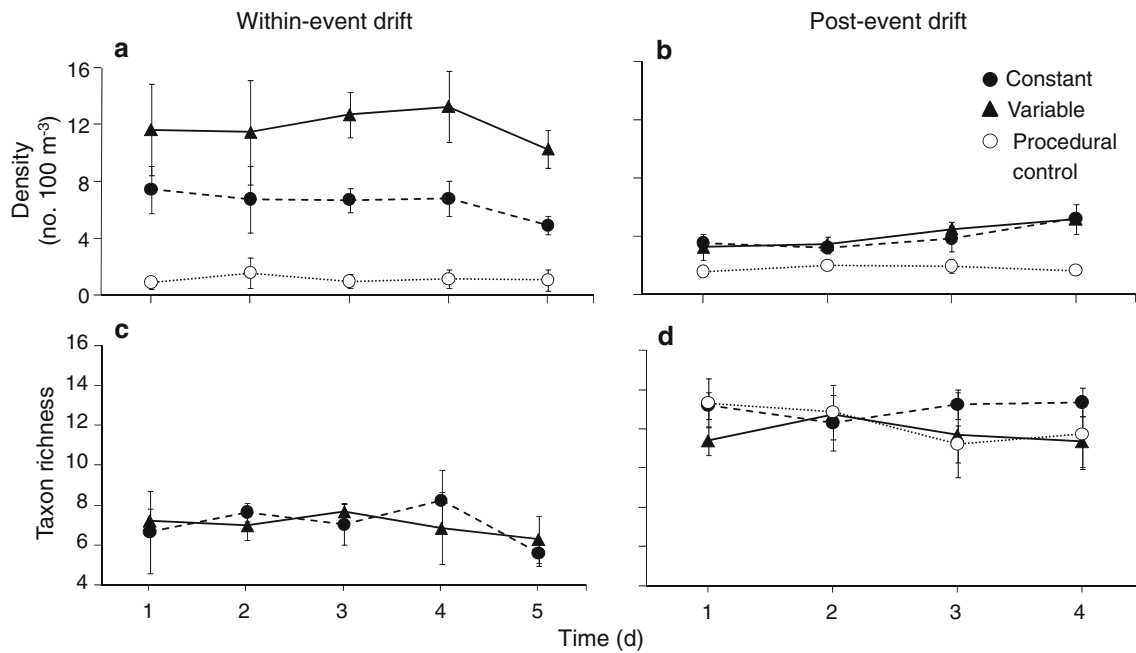


Fig. 3 Densities (a, b) and rarefied (c, d) taxon richness of invertebrates drifting from experimental channels during sediment addition (a, c; within-event drift) and during the time elapsed between consecutive pulses (b, d; post-event drift) for the variable, constant and pro-

cedural control treatments (mean ± SD, n = 3). Results from the procedural controls were not included in the calculation of rarefied richness of within-event drift because of the low sample size. d Days

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

Constant vs. variable		Variable vs. control		Constant vs. control	
Principal invertebrate taxa	Percentage contribution	Principal invertebrate taxa	Percentage contribution	Principal invertebrate taxa	Percentage contribution
Chironomidae (Diptera; CG)	15.2	Simuliidae (Diptera; CF)	26	Simuliidae (Diptera; CF)	26.4
Simuliidae (Diptera; CF)	14.4	Chironomidae (Diptera; CG)	18.8	Chironomidae (Diptera; CG)	15.2
<i>Chaetopteryx villosa</i> (Trichoptera; SH)	8.5	<i>Leuctra inermis</i> (Plecoptera; SH)	10.3	<i>Protonemura meyeri</i> (Plecoptera; SH)	11.4
<i>Siphonoperla torrentium</i> (Plecoptera; P)	8.2	<i>Protonemura meyeri</i> (Plecoptera; SH)	9.4	<i>Leuctra inermis</i> (Plecoptera; SH)	11.2
<i>Protonemura meyeri</i> (Plecoptera; SH)	7.8	<i>Siphonoperla torrentium</i> (Plecoptera; P)	7.2	<i>Siphonoperla torrentium</i> (Plecoptera; P)	7.3
<i>Leuctra inermis</i> (Plecoptera; SH)	7.3	<i>Amphinemura sulcicollis</i> (Plecoptera; SH)	5.5	<i>Amphinemura sulcicollis</i> (Plecoptera; SH)	6.8
<i>Amphinemura sulcicollis</i> (Plecoptera; SH)	6.1	<i>Chaetopteryx villosa</i> (Trichoptera; SH)	4.6	<i>Chaetopteryx villosa</i> (Trichoptera; SH)	5.9
<i>Limnius volckmari</i> (Coleoptera; S)	4.7	<i>Rhyacophila munda</i> (Trichoptera; P)	3.2	<i>Limnius volckmari</i> (Coleoptera; S)	3.4
<i>Rhyacophila munda</i> (Trichoptera; P)	4.7				
<i>Rhyacophila dorsalis</i> (Trichoptera; P)	4.1				

Constant, treatment regime comprising press pulses where a constant sediment dosage was maintained for the duration of the disturbances; variable, treatment regime comprising ramped pulses in which the sediment dosage decreased consistently over the total length of the disturbances
SIMPER Similarity percentages analysis, SH shredder, CG collector–gatherer, CF collector–filterer, P predator, S scraper

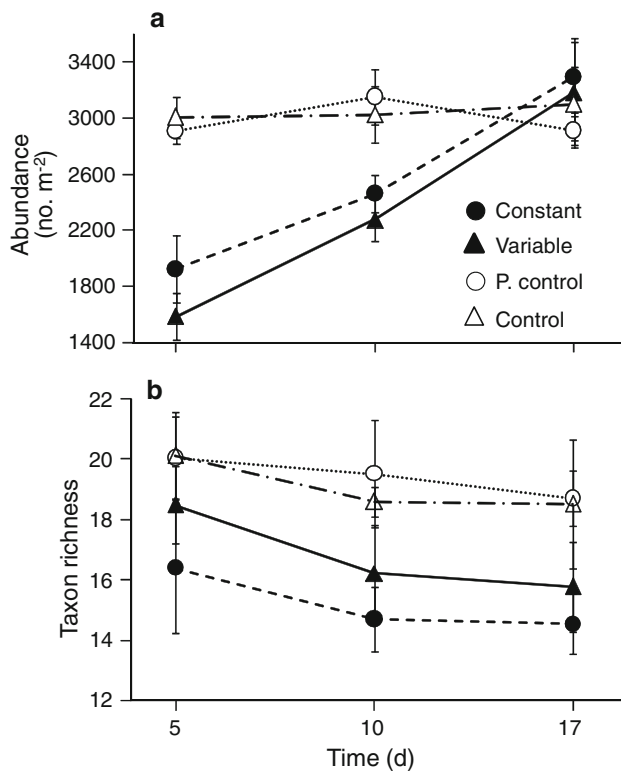


Fig. 4 Abundance (a) and rarefied taxon richness (b) of benthic invertebrates in situ immediately following the cessation of sediment disturbances (Day 5) and during the subsequent recovery period (Day 10, Day 17) for the variable, constant, procedural control and control treatments (mean \pm SD, $n = 3$)

treatments ($p < 0.05$), but no difference was found between the constant and variable disturbance treatments.

Benthic invertebrates in situ

Both the abundance (Table 1; Fig. 4a) and trophic structure (Table 2; Fig. 5b) of benthic assemblages in situ were 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 (i.e. constant and variable treatments) was, however, significantly lower ($p < 0.05$) than in the two control treatments—both immediately (Day 5) and 5 days following the last disturbance (Day 10). 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 12 days after the final disturbance (Day 17; Fig. 4a).

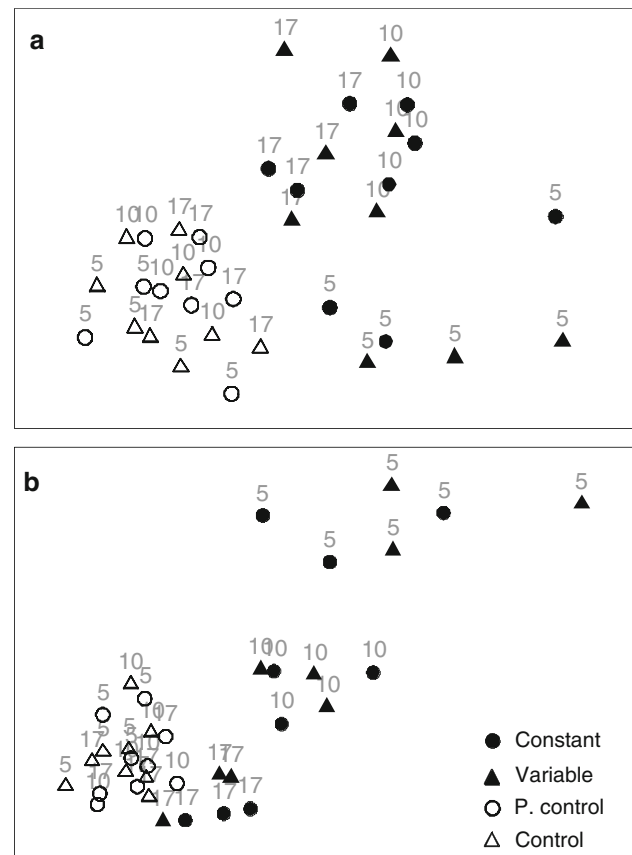


Fig. 5 Non-metric multidimensional scaling (nMDS) plots showing differences in the taxonomic composition (a; stress = 0.16) and trophic structure (b; stress = 0.07) of invertebrate assemblages in situ after cessation of disturbances. Number with each symbol indicates the corresponding sampling day (Day 5 corresponds to the final day of experimental disturbance)

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

Both taxon richness (Table 1; Fig. 4b) and taxonomic composition (Table 2; Fig. 5a) of benthic assemblages in situ varied significantly among experimental treatments. 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 disturbed treatments, even though the taxon richness in the variable treatment was consistently higher than that in the constant disturbance treatment for the duration of the experiment (Fig. 4b).

Discussion

Our 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. We found significantly different responses of benthic invertebrate assemblages to our ‘press’ (constant) and ‘ramped’ (variable) pulse disturbances even though the mean intensity, duration, frequency and timing of the perturbations were 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 (e.g. Butler 1989; Sommer 2000; Benedetti-Cecchi et al. 2006; García Molinos and Donohue 2010). 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 our experimental channels. Large-scale displacements of invertebrates occur commonly under increased sediment loading (e.g. Culp et al. 1987; Shaw and Richardson 2001). However, in our experiment we also found remarkably different drift responses between those occurring during disturbances (within-event drift) and those taking place among disturbances (post-event drift). This suggests strongly that the mechanisms behind those responses differed. Drift densities during the temporally variable disturbances were almost double those from the constant perturbations. Moreover, this is likely to be a conservative estimate of the magnitude of the differences in patterns of drift between the two disturbed treatments as drift responses to abrupt pulsed disturbances often occur rapidly (i.e. within minutes from the start of the perturbation; Gibbins et al. 2010). By integrating drift numbers over the 3-h duration of the sediment pulse, our estimates of drift density could well underestimate potentially more dramatic differences between the disturbed treatments in the response of the within-event drift. Moreover, the composition and trophic structure of 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 within-event drift response. The greater maxima and higher variability of sediment loading achieved under the variable disturbance treatment likely 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; Gibbins et al. 2007b), thereby increasing physiological impairment owing to the clogging of respiratory and feeding body structures (Lemly 1982; Broekhuizen

et al. 2001) or by triggering drift indirectly by, for example, augmenting light attenuation (Waters 1995). The fact that the principal taxa contributing to control versus disturbance differences in the composition of within-event drift remained largely the same for the two disturbed treatments suggests 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 within-event drift.

We found no differences between the two disturbed treatments in the densities or composition of drift among perturbations. Post-event drift densities 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 through indirect factors, such as reduced food quality and availability (Suren 2005; Peeters et al. 2006) or changes in substrate composition (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 post-event drift response. We found, however, evidence that taxon richness of the post-event drift was higher in the constant than in the variable disturbance treatment. Ecological responses to disturbance are often conditioned by previous stress history (e.g. Ruane et al. 2002). This result indicates that varying temporal patterns during perturbations may differentially affect invertebrate drift even after the disturbances have taken place.

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; García Molinos and Donohue 2009, 2010). However, even though benthic assemblages *in situ* under both disturbed 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. Although the mechanisms behind this difference, likely linked to those of the drift, are difficult to establish, its 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; Fraterrigo and Rusak 2008). The development and testing of current theories requires 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

(Lake 2000; Roxburgh 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 et al. 2001) or to use a constant value over the duration of a perturbation (e.g. 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 demonstrated how the rate of change in intensity during a disturbance event mediates its effect on biological communities, with abrupt changes producing typically stronger effects on exposed communities than gradual changes. However, the effects of the temporal pattern of disturbance in these studies were confounded with those of other disturbance attributes. Our experimental design enabled the analysis of the effects of temporal patterns of disturbance independent of other characteristics of disturbances. Our 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 equal.

Our findings have important practical implications. Temporal patterns of pollutant concentrations in rivers depend on both the type and source of pollutant and can vary considerably both within and among ecosystems and even among seasons (Donohue et al. 2005). For example, loads of fine inorganic sediment from terrestrial soil erosion, which comprises one of the most pervasive anthropogenic disturbances affecting aquatic ecosystems worldwide (Donohue and García Molinos 2009), typically follow the bell-shaped storm flow hydrograph (e.g. Lisle 1989), whereas activities such as flushing maintenance operations (e.g. Banas et al. 2008; Gomi et al. 2010) or extractive operations (e.g. Krishnaswamy et al. 2006) tend to generate a ‘ramp’-shaped pattern similar to that used in our experiment. Current environmental management is heavily reliant on the definition of ecological thresholds to establish a point beyond which ecosystem deterioration occurs (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); critical loads in the 1979 Geneva UNEC Convention of Long-Range Transboundary Air Pollution]. Monitoring programmes 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 on the way in which organisms have been exposed to disturbances. Understanding which mechanisms underlie apparent threshold behaviour is critical for the sensible application of thresholds (Groffman et al. 2006). Our results suggest strongly that the quantification of the temporal patterns within as well as among perturbations would considerably advance such an understanding.

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