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# Hydrology, hydraulics and scale influence macroinvertebrate responses to disturbance in tropical streams

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**ABSTRACT**

Despite much research on the influence of disturbance on stream macroinvertebrates, comparative information on tropical streams is limited. We assessed disturbance influence on assemblages under different conditions of hydrology (aseasonal and seasonal) and hydraulics (pools, riffles and stream morphology) by sampling a stream in the Australian Wet Tropics (AWT) pre- and post-flood, and by undertaking experiments at whole-riffle and single-stone scales in several streams in the AWT and Papua New Guinea (PNG). The fauna was very mobile in all streams, facilitating recolonisation. Resilience (recovery) was strongly related to scale – rapid in single-stone experiments (2–4 d) and least following whole-stream disturbance (~45 d, comparable with some temperate systems), indicating the importance of scale in understanding disturbance. Local undisturbed patches and pools acted as refugia and provided colonists at least partly via drift. The presence of all life stages of most species through the year and rapid development would facilitate recovery. Multiple disturbances had similar impact to single events, resulting in a reduced but resilient fauna. Resilience was not greatly different in more regularly disturbed sites, but richness was lower in PNG than AWT possibly due to their different disturbance regimes. Disturbance selects a sustained fauna that is resilient (or tuned) to the prevailing disturbance regime.

## Introduction

Understanding how biotic assemblages respond to natural disturbance is important in developing models of community dynamics and ecosystem processes, and is especially relevant to understanding the ecological impacts of anthropogenic disturbance (Stanley et al. 2010; Nimmo et al. 2015). Most streams worldwide are regularly disturbed by discharge events that mobilise stream substrates, representing pulse disturbance (Lake 2000), with substantial influence on the biota (e.g. Resh et al. 1988; Pearson 2014). Variability in the physical environment provides strong selective forces for ecological strategies and response mechanisms that enable local species persistence (Poff and Ward 1990), and disturbance modifies the stochastic and deterministic processes that interact in controlling assemblage composition (Thompson and Townsend 2006; Lepori and Malmqvist 2009). As hydrological unpredictability increases, species with traits conferring resistance (e.g. firm attachment, flexible body forms, streamlining or flattening) or resilience (e.g. use of refugia, high mobility, small size and rapid development) are predicted to be selected (Townsend and Hildrew 1994). Populations and assemblages from environments with more variable flow regimes should therefore be less

susceptible to disturbance, as it selects for a disturbance-tolerant biota, than those from more constant environments (Poff and Ward 1990) and will show high persistence through resistance or resilience mechanisms (Calderon et al. 2017).

High-flow disturbance in streams includes tumbling of individual stones and abrasion by suspended sediment, causing fauna to be dislodged or damaged. The interaction of stream flow with substrates determines the frequency of disturbance, which provides an indicator of habitat stability (Reice et al. 1990; Townsend et al. 1997a) and disturbance history (Effenberger et al. 2006; Woodward et al. 2015). The velocity required to move particles increases with their mass, except that fine particles (silt and clay) require high velocities to overcome adhesive forces (Ambuhl 1959). Because the spates required to move silts and boulders are typically less frequent than smaller events, substrates with intermediate particle sizes are predicted to have the highest frequency of disturbance, and consequently support the most disturbance-tolerant assemblages (Reice et al. 1990). The local disturbance regime, habitat heterogeneity and resilience of assemblages (Matthaei et al. 1996; Palmer et al. 1996) thus all influence the within-stream distribution of benthic invertebrates.

The incorporation of disturbance into concepts of stream ecosystem structure and function is based largely on many temperate-zone studies, which were developed in the 1980s and 1990s (Stanley et al. 2010), but continue to generate research interest (e.g. Robinson 2012; Peckarsky et al. 2014; Woodward et al. 2015; Bruno et al. 2016). While the effects of natural disturbance on stream fauna may be universal (Vinson and Hawkins 2003; Boulton et al. 2008), evidence for the tropics is limited. For example, a global meta-analysis of invertebrate resistance to floods in 41 streams included only one tropical site (McMullen and Lytle 2012). Further, stream characteristics (e.g. flow regime) that vary across the tropics (Yule and Pearson 1996) are likely to present a range of disturbance environments, as is the case in other zones (Boulton et al. 2008). To fully understand stream disturbance ecology globally, it is important that we understand the variation in faunal responses that may occur in different climatic, geomorphic and hydrological settings (Jacobsen and Encalada 1998; Vinson and Hawkins 2003; Stanley et al. 2010; Astorga et al. 2011; Stroud and Feeley 2017). Studies on disturbance ecology in tropical streams are increasing, but typically relate to anthropological disturbance (e.g. Benstead et al. 2003; Dudgeon 2006; Ligeiro et al. 2013). Tropical studies are mostly observational (e.g. Datry et al. 2016) with the few experimental studies reported indicating that recovery from disturbance at small scales is rapid (e.g. Rosser and Pearson 1995; Boyero and DeLope 2002).

We evaluated disturbance influence on tropical stream macroinvertebrate assemblages under different disturbance regimes at three scales using a combination of experimental and observational studies. Experimental studies on stream disturbance typically focus on small-scale movement of substrates (e.g. Robinson et al. 2011; Herrmann et al. 2012). While small-scale experiments can be a problem if not in a proper context (Englund and Cooper 2003; Scholes 2017), they can adequately simulate flood effects on invertebrates (Matthei et al. 1997) and are considered the appropriate scale for examining community recovery (Death 1996). In this study, we measured the responses of macroinvertebrates to natural and experimental disturbance at individual stone (microhabitat), whole riffle/pool (mesohabitat) and whole-stream (macrohabitat) scales, in different hydraulic habitats and under different hydrological regimes in rainforest streams of the Australian Wet Tropics (AWT) and Papua New Guinea (PNG) (Table 1). We made several predictions, as follows:

(1) We monitored assemblages in riffles and pools through periods of stable flow and substrate-shifting flood. We predicted that pools would provide a disturbance refuge (e.g. Benson and Pearson 1987b; Brooks et al. 2017)…
(2) … but that recovery would not be rapid at this scale (Gjerløv et al. 2003; Pearson 2014).
(3) We examined assemblage responses to experimental disturbance of stones in pools and riffles in an upland and a lowland stream and at three hydraulically different sites along a single stream, predicting rapid recovery at this stone scale (e.g. Rosser and Pearson 1995)…

**Table 1.** Outline of observations and experiments undertaken in pools and riffles of nominated AWT and PNG streams, described in this paper, classified by disturbance scale and prevailing flow regime at the time of the experiment. 'Yucc.' = Yuccabine Creek. Numbers in square brackets indicate predictions (outlined in Introduction) being tested.

| | Disturbance scale | | |
|---|---|---|---|
| Prevailing flow | Whole stream (field observations) | Riffle (field experiments) | Stone (brick) (field experiments) |
| High | Birthday riffle 1 [1, 2, 7] Birthday riffle 2 [1, 2, 7] | Tam (PNG) riffle 1 [6, 7] Tam (PNG) riffle 2 [6, 7] Ck 115 (PNG) riffle [6, 7] | |
| Moderate | Birthday pool 1 [1, 2, 7] Birthday pool 2 [1, 2, 7] | Birthday riffle [6, 7] | Yucc upper riffle [3, 4, 7] Yucc. mid riffle [3, 4, 7] Yucc lower riffle [3, 4, 7] Birthday riffle [3, 5, 7] Pixies riffle [3, 7] |
| Low | | | Birthday pool [3, 5, 7] Pixies pool [3, 7] |

(4) ... but lower resilience in sites that were hydraulically more benign (e.g. low slope) and perhaps more susceptible to disturbance (e.g. Death 1996).

(5) We investigated the responses of the stone fauna to multiple experimental disturbances in a pool and a riffle, predicting cumulative effects, leading to a reduced but resilient fauna.

(6) We examined assemblage responses to experimental disturbance of stones in streams in the AWT and PNG with respect to their contrasting hydrology (seasonal vs. aseasonal), predicting a reduced but more resilient fauna in the more regularly disturbed PNG streams (Death 1996).

(7) We compared the results of these observations and experiments to assess the effect of scale of disturbance at whole stream (macrohabitat), whole riffle (mesohabitat), and stone (microhabitat) scales on the responses of macroinvertebrates, predicting recovery to be inversely related to scale.

In this paper, we use 'resilience' to include 'resistance', except where explained otherwise, because discriminating between them is scale- and time-dependent – for example, resistance traits not only involve animals remaining attached to the substratum but may include withdrawing into the substratum or rapid dispersal (Townsend et al. 1997a), possibly manifesting as resilience following disturbance.

## Methods

### Study locations

The study streams were located in the AWT bioregion of north-eastern Queensland and in the Fly River catchment in equatorial PNG (Table 2; Supplementary Information, Figure S1). The two regions differ in rainfall and flow regimes – seasonal in the AWT and aseasonal in PNG (Yule and Pearson 1996) – and, consequently, in stream disturbance frequency. Stream discharge is closely correlated with daily rainfall in both regions (Clayton and Pearson 2016; unpublished data) so we used monthly rainfall coefficient of variation (CV) as a measure of flow disturbance (Vinson and Hawkins 2003). In the AWT, unpredictable high flows occur in the wet season (November to March), followed by stable low flows in the dry season (Pearson 2014). In PNG, flows have high day-to-day variability but low monthly variability (Yule and Pearson 1996) (Table 2).

The AWT study sites were Birthday and Yuccabine Creeks in the uplands, and Pixies Creek in the lowlands, all having characteristics of other AWT low-order forest streams (Pearson et al. 2017). The PNG sites were lowland low-order forest streams, Tam Creek and Creek 115, tributaries of the

**Table 2.** Physical characteristics of the study sites in the Australian Wet Tropics (Birthday Creek, Yuccabine Creek, and Pixies Creek) and Papua New Guinea (Tam Creek and Creek 115). Climate data from Australian Bureau of Meteorology (AWT) and http://en.climate–data.org/location/19237/ (PNG). '–' indicates data unavailable.

| | Australian wet tropics | | | | | Papua New Guinea | |
| | | Yuccabine | | | | | |
| | Birthday | Upper | Mid | Lower | Pixies | Tam | 115 |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Location °S, °E | 18.99, 146.17 | 18.19, 145.77 | 18.21, 145.76 | 18.21, 145.77 | 17.78, 145.68 | 5.37, 141.29 | 5.45, 141.29 |
| Altitude (m asl) | 800 | 750 | 640 | 614 | 60 | 340 | 240 |
| Slope (%) | 1.1 | 4.3 | 2.2 | 1.7 | 6.1 | 7.0 | 4.8 |
| Annual rainfall (mm) | 2497 | 2073 | 2073 | 2073 | 3865 | 6194 | 6194 |
| Rain monthly CV (%) | 88.0 | 89.4 | 89.4 | 89.4 | 68.7 | 10.4 | 10.4 |
| Rain daily mean Nov/Feb (mm) | 0.3/35.0 | – | – | – | – | 15/19 | 15/19 |
| Rain daily CV (%) Nov/Feb | 18/1577 | – | – | – | – | 110/117 | 110/117 |
| Shade % | 70 | 35 | 40 | 30 | 55 | 20 | 40 |
| Stream order | 3 | 2 | 3 | 3 | 3 | 3 | 4 |
| Mean width (m) | 7.5 | 5.0 | 7.0 | 10.0 | 7.0 | 4 | 4 |
| Mean depth (m) | 0.45 | 0.4 | 0.45 | 0.35 | 0.5 | 0.40 | 0.30 |
| Mean water temperature (°C) | 20.5 | 19.5 | 20.0 | 20.5 | 20.5 | 24.0 | 24.0 |
| Dominant substratum (Φ scale: sand, −1 to 3; stone, −6 to −7; boulder, -8 to −9) | Stone/gravel | Stone/boulder | Stone | Stone/sand | Stone/boulder | Stone | Stone |
| Mean substrate size (mm) | 150 | 212 | 144 | 33 | 235 | ∼200 | ∼200 |

Ok Tedi River, which had similar characteristics to the AWT streams, apart from their contrasting hydrographs. All sites had substrata that included a large proportion of loose stones; slopes were higher in the PNG than the AWT streams (Table 2).

## Natural assemblage fluctuations and whole-stream (macrohabitat) disturbance

We investigated the resilience of assemblages to natural whole-stream disturbance in Birthday Creek, by sampling stone fauna from a 100-m riffle over 43 months and a 25-m pool over 16 months. Here we focus on data from before and after two floods. Post-flood samples were collected 21 and 6 days following the floods (January 1994 and February 1995, respectively; the post-flood timing of sampling was dictated by availability of access). We gauged movement of the substratum by measuring the displacement of clay bricks caused by the second flood (cf. Townsend et al. 1997a). Bricks had dimensions of 0.14 × 0.14 × 0.08 m and a surface area of 0.08 m$^2$, and were of similar density to natural stones (Rosser and Pearson 1995). We sampled the fauna each month from eight randomly selected natural stones (∼ 0.16 m diameter, 0.08 m$^2$ surface area) from each habitat by gently lifting them into a dip net (250 μm mesh) held downstream. Macroinvertebrates were removed from the stone surface using a test-tube brush, and were preserved in 70% ethanol. The stone was weighed and its surface area was estimated from a previously determined regression (Rosser and Pearson 1995). In the laboratory, macroinvertebrates were identified, mostly to genus or species, except for early-instar larvae and Chironomidae and Oligochaeta, and counted.

## Experimental stone-scale (microhabitat) disturbance: contrasting hydraulics

We used bricks (as above) for these experiments because they were readily identifiable and good surrogates for natural stones following four weeks' conditioning (Rosser and Pearson 1995), and because we expected them to provide a realistic simulation of flood effects on the invertebrate assemblage (Matthei et al. 1997). Thirty-two bricks were placed in riffles and pools in Birthday and Pixies creeks. After four weeks, bricks were disturbed in situ, according to each treatment (each with eight replicates) – control (no disturbance), low (bricks tumbled twice), medium (bricks tumbled 10 times) and high (bricks tumbled 10 times and scrubbed with a test-tube brush) – then replaced on

the streambed for 24 h. On retrieval, each brick was collected in the dip net and macroinvertebrates were removed and preserved as above.

To represent a gradient in geomorphology and hydraulics, we selected three riffle sites along Yuccabine Creek: a narrow higher-slope headwater site ('upper'), a wider, lower-slope lower site ('lower') and an intermediate site ('middle'), which was similar in size to the Birthday and Pixies creek sites and had been the focus of other studies (e.g. Pearson 2014). Pre-conditioned bricks were labelled according to their designated treatments and sampled following disturbance as above.

The cumulative effect of multiple disturbances was determined at Birthday Creek using pre-conditioned bricks and four treatments, as above, in the riffle ($N = 160$) and pool ($N = 64$). For the riffle, following the four-week conditioning period, all bricks were disturbed weekly for five weeks, according to their treatments; 24 hr after disturbance, eight bricks from each treatment were collected. For the pool, the procedure was similar but collections were made only at weeks 3 and 5. Macroinvertebrates were removed from each brick and preserved as above.

### Experimental riffle-scale (mesohabitat) disturbance – contrasting hydrology

To assess faunal responses to whole-riffle disturbance under contrasting hydrological conditions, we conducted experiments in Birthday Creek (October 1993) and in the PNG streams –Tam Creek (August 1993, December 1994) and Creek 115, (December 1994). Sampling of Birthday Creek was undertaken in the dry season, under stable hydrological conditions, to contrast with the regular spates of the PNG streams. During our PNG experiments, up to 75 mm of rainfall occurred most days. The experimental disturbance involved vigorous raking of the substratum in each entire riffle with a steel-tined rake, working downstream, tumbling all stones and removing leaf accumulations. Eight stones ($\sim 0.08$ m$^2$) were sampled within 4 hr of the experimental disturbance (day 0), then at 2-d intervals to day 8 (1993 samples) or day 14 (1994 samples), as described above. On each occasion, eight stones were sampled from an undisturbed riffle in each stream, as controls.

Macroinvertebrate drift was sampled at Tam Creek and Birthday Creek during 17.5 hr before and 4 hr immediately after the experimental disturbance (1400–0730 hr and 11.30–1530 hr). Drift nets consisted of a conical collecting net (250 µm mesh) connected to an aluminium frame (0.02 m$^2$ inlet). Three nets were fixed to metal stakes 10 cm above the substratum at the downstream end of each riffle. Current velocity was measured at each net using an OSS flow meter, and filtered volume was estimated from the product of area of net opening, current velocity and duration of sampling. Samples were preserved in 70% ethanol and returned to the laboratory for processing. Drift was expressed as density per m$^3$ of water filtered.

### Data analysis

Macroinvertebrate density per stone or brick was expressed as individuals per 0.08 m$^2$ and was transformed to log ($x + 1$) for analysis. Means were compared using paired $t$-test or ANOVA followed by Tukey tests ($\alpha = 0.05$) in SPSS$^{TM}$; for time series we used repeated-measures ANOVA. Assemblage data were ordinated by multidimensional scaling in PC-ORD (McCune and Mefford 2011), using taxa that contributed $> 0.05\%$ of overall totals. Multi-response permutation procedures (MRPP) were undertaken in PC-ORD to test for differences between disturbed and control assemblages. Assemblage resistance was quantified as the change in density and richness caused by the experimental disturbance (Fisher and Grimm 1988), and by comparing degree of displacement in ordination space between disturbed and control assemblages. Taxa were considered resistant if their numbers did not decline significantly immediately following disturbance. Resilience was measured as the time taken to attain similar density and richness on disturbed and control stones, and for the development of similar assemblage structure, according to ordination plots. An indicator of relative resilience between sample types was derived from the mean recovery period (days) for density and richness. We multiplied $\times 10$ the reciprocal of the square root of this mean to simplify presentation.

## Results

Over all samples, there was an asymptotic relationship between richness and density, such that in many cases, especially in the AWT, loss of richness was a reflection of density reduction (Supplementary Information, Figure S2).

### *Natural assemblage fluctuations and macrohabitat disturbance (Birthday Creek)*

In Birthday Creek, 73 taxa were collected from the riffle and 50 from the pool (Supplementary Information, Table S1). The predominant taxa were, in the riffle, *Simulium* sp., Chironomidae, Oligochaeta, *Kingolus* sp. and *Dinotoperla* sp. and, in the pool, Chironomidae, Oligochaeta, *Austrophlebioides* sp. and *Baetis* sp. The smaller (1995) flood resulted in the downstream displacement of bricks by 3.07 m $\pm$ 0.85 m, so the two floods were of sufficient intensity to substantially alter the physical habitat of Birthday Creek. Repeated-measures ANOVA indicated no flood effects, although Tukey's tests indicated that the first flood reduced abundance and both floods reduced richness in the riffle, while in the pool neither flood affected abundance but both increased richness (Figure 1(a–c); Supplementary Information, Table S2). Where effects were apparent, densities and richness were at pre-flood levels within about 45 d following the floods. Many taxa had high resilience to the floods in the riffle, with post-flood densities not significantly different from pre-flood levels, and most species had a consistent response to the two floods (Supplementary Information, Table S2). An exception was the Chironomidae, which were depleted following the larger flood but not after the smaller flood. Within-sample variation (CV) increased following both floods for the majority of taxa, regardless of whether resilience was high or low. Resilience appeared greatest in the pool, with density and richness no different 21 d following the larger flood, and higher 6 d following the smaller flood. Ordination of the riffle samples (Figure 1(d)) showed that there were distinct shifts between pre- and post-flood samples, following the same trajectory, with a similar pattern for the pool (Figure 1(e)). Change in assemblage composition was higher following the smaller flood, probably because the sample was taken sooner after the flood.

### *Experimental microhabitat disturbance – contrasting hydraulics (Birthday, Pixies and Yuccabine Creeks)*

The low, medium and high disturbance treatments removed 40%, 87% and 98% of all macroinvertebrates and 35%, 50% and 75% of taxa, respectively (Table 3). Even the low treatment removed individuals of most taxa, both mobile and sedentary (e.g. respectively, *Baetis* sp., *Helicopsyche* sp.). The individuals present at the time of sampling thus represent a combination of local resistance (i.e. those individuals remaining) and resilience/mobility (individuals colonising within 24 h), with mobility assuming greater importance on medium and high treatments.

Density and richness on the control bricks were higher in the riffle at Birthday Creek than at Pixies Creek but lower in the pool (Figure 2(a,b)). Disturbance intensity did not affect richness in the riffle or pool in either stream. Density was not reduced by the treatments in the Birthday Creek riffle, but was reduced by the higher treatments in the Pixies Creek riffle and in the pools in both streams. Ordination shows that, in the riffles, the disturbance caused somewhat greater change in assemblages at Pixies Creek than at Birthday Creek, while in the pools changes were similar in extent between streams though largely opposite in direction on Axis 1 (Figure 2(c,d)).

In the repeated disturbance experiment at Birthday Creek, disturbance reduced density and richness in the riffle and pool in each of the weekly treatments (Figure 3(a,b)). However, there was little change in pattern with repeated disturbance over five weeks: although Tukey tests showed contrasts, in a repeated-measures ANOVA only richness in the riffle following the High treatment was significant ($F_{4,28} = 2.56$, $P = 0.0361$; Table S5).
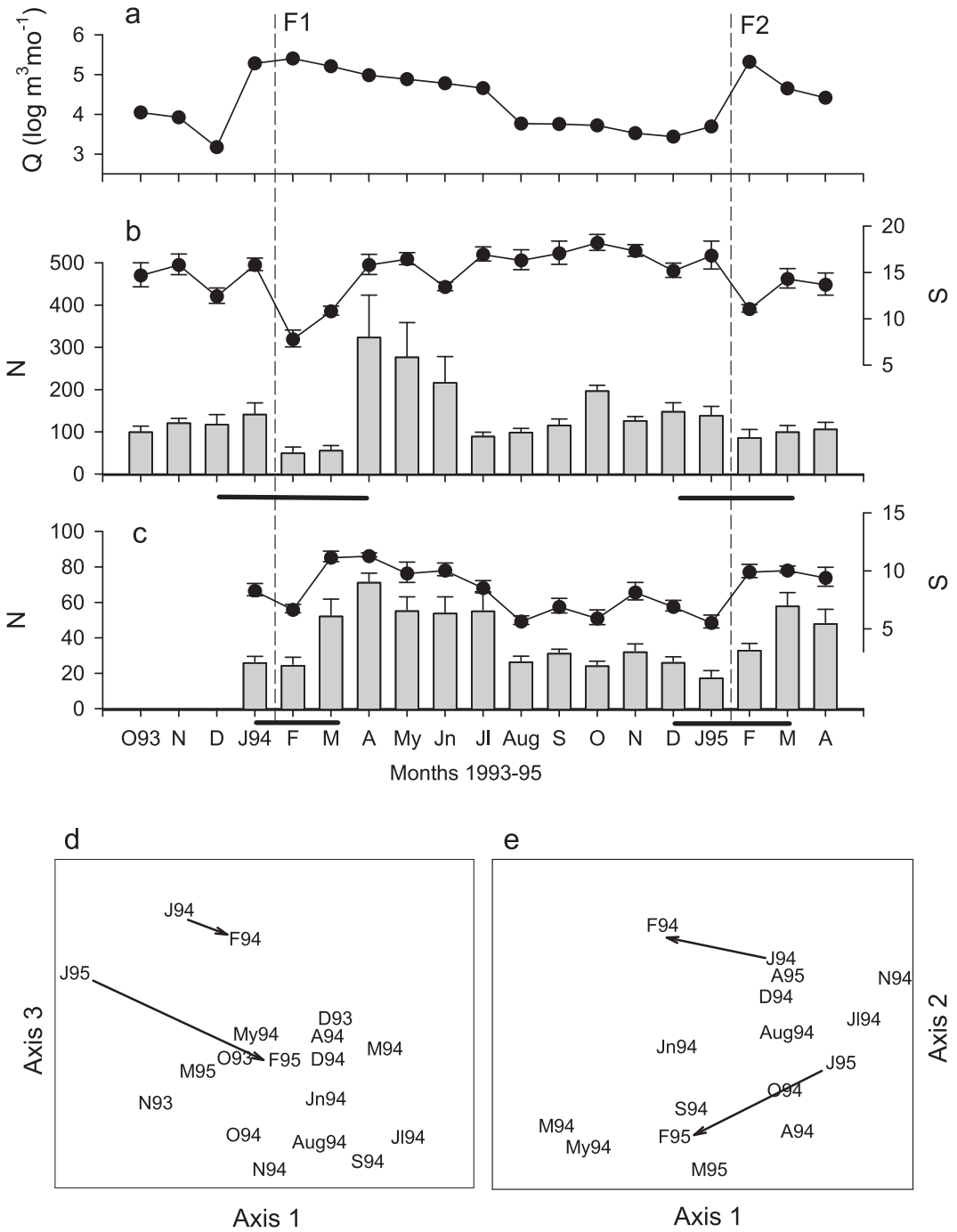
**Figure 1.** (a) Monthly flow in Birthday Creek, with timing of flood peaks (F1 and F2) indicated by dashed lines; (b) macroinvertebrate density (N) and richness (S) on riffle stones; (c) density and richness on pool stones; and (d) ordinations of assemblages in riffles and (e) pools. Density and richness are expressed per stone (0.08 m$^2$) ± S.E. Daily flood peaks were 150,451 m$^3$ (F1, 31 January, 1994) and 45,359 m$^3$ (F2, 11 February, 1995) (Pomeroy 1998). Horizontal bars under X axis in (b) and (c) indicate samples included in flood-specific repeated-measures ANOVAs. Samples taken before and after the two floods are linked by arrows in (d) and (e).
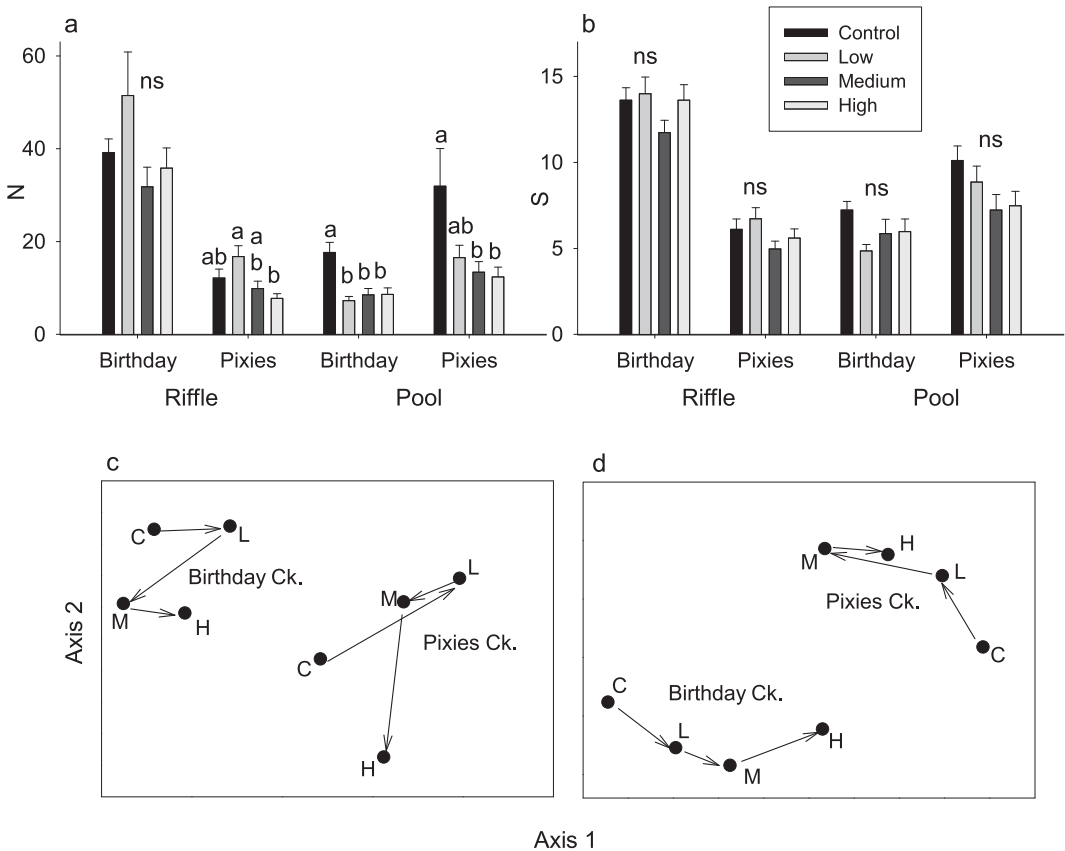
**Figure 2.** Effects of four disturbance treatments (control, low, medium and high) in riffles and pools in Birthday and Pixies creeks on stone-dwelling macroinvertebrate density (a) and richness (b), showing means ± S.E. per stone (half brick); and ordination of assemblages resulting from each treatment in riffles (c) and pools (d). In (a) and (b) significant differences between samples within streams and habitats (post–ANOVA Tukey tests, $\alpha = 0.05$) are indicated by letters above each column; ns = not significant. ANOVA results are given in Supplementary Information, Table S5.

The Yuccabine Creek headwater site had lower density than the other Yuccabine Creek sites, while the mid-reach site had higher richness (Figure 4(a,b)). At the headwater site, only the high disturbance treatment affected density, and none affected richness; the mid-reach site was the most affected by the treatments, with the greatest reductions in density and richness; at the lower site, disturbance caused a moderate decline in richness, but no significant change in density (Figure 4(a,b)). Ordination of the assemblages separated the mid-reach site from the headwater and lower-reach sites on Axis 1 (Figure 4(c)). Changes due to disturbance largely followed similar trajectories and showed that assemblages were most altered by disturbance at the intermediate site and least altered at the lower site.

### *Experimental whole-riffle (macrohabitat) disturbance – contrasting hydrology (Birthday and Tam Creeks and Creek 115)*

Tam Creek was dominated by *Baetis* species and Chironomidae; at Creek 115, the same mayflies were present but *Agapetus* sp. 1 (Glossosomatidae) and chironomids were predominant. The most common taxa at Birthday Creek included Chironomidae, Simuliidae and Plecoptera, the latter being absent from the PNG steams (Supplementary Information, Table S3). On day 14 in 1994, flow levels of the PNG streams were elevated from an overnight spate, and several

Table 3. Effect of experimental disturbance treatments (low, medium, high) on common macroinvertebrate taxa and the overall assemblage, expressed as the proportion (%) of individuals of each taxon removed from the bricks following each treatment, in Birthday Creek. '–' indicates taxa that were rare or absent from treatment.

| Taxon | Low | Medium | High |
|---|---|---|---|
| Lepidoptera sp. 1 | 0 | – | – |
| Tipulidae sp. 3 | 0 | – | 98 |
| Helicopsyche sp. | 100 | – | – |
| Austrophlebioides sp. 1 | 75 | 100 | – |
| Baetis sp. | 100 | 100 | 100 |
| Tasmanocoenis sp. | 96 | 100 | 100 |
| Hydroptilidae, early instars | 71 | 96 | 93 |
| Simulium sp. | 60 | 100 | 100 |
| Oecetis sp. 1 | 60 | 100 | 100 |
| Nyctiophylax sp. | 30 | – | – |
| Hydroptilidae sp. 1a | – | 75 | 100 |
| Hydroptilidae sp. 2 | – | 86 | 100 |
| Hydroptilidae sp. 3 | 50 | 83 | 94 |
| Oligochaeta | 34 | 99 | 100 |
| Chironomidae | 30 | 81 | 97 |
| Helminthidae (l) sp. 2a | – | 82 | 100 |
| Kingolus sp. | – | 89 | 94 |
| Dinotoperla sp. | – | 50 | 100 |
| Reduction in overall abundance | 40.0 | 87.0 | 98.0 |
| Taxa removed | 35 | 50 | 75 |
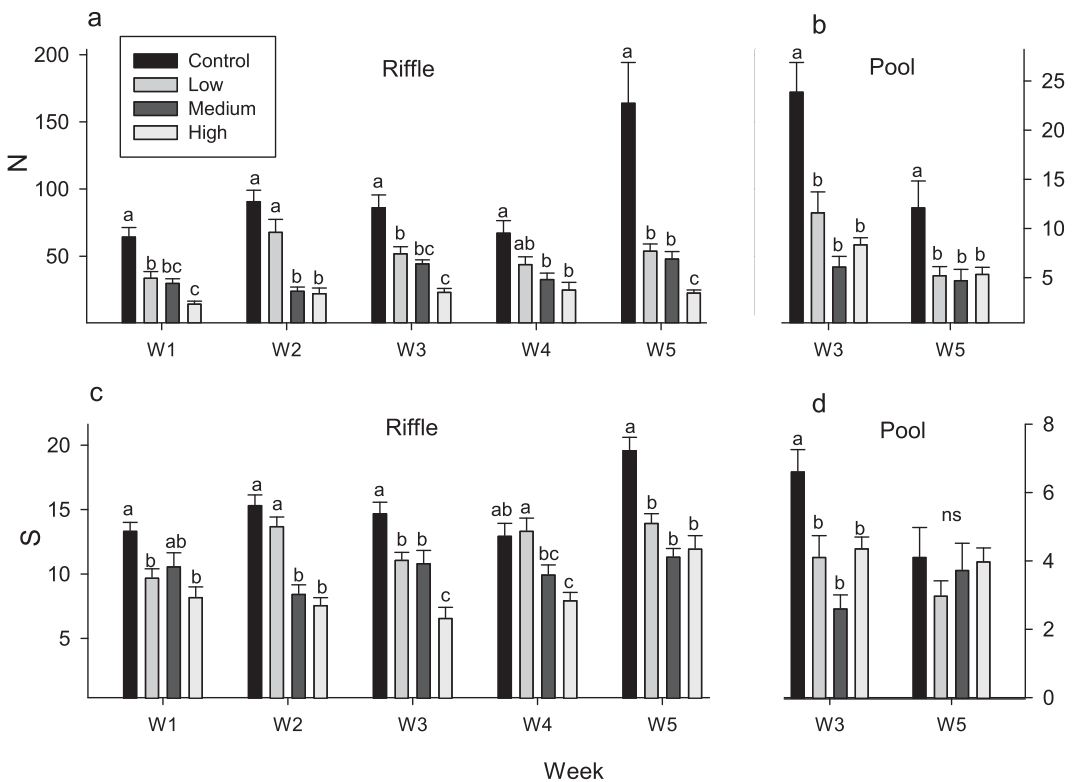


Figure 3. Effects of repeated disturbance treatments (control, low, medium and high) on stone assemblage density (a, b) and richness (c, d) in a riffle and pool in Birthday Creek following 1 to 5 weekly disturbance events (W1–W5, respectively). Density and richness are expressed per stone (0.08 m$^2$) ± S.E. Note different scales for riffle and pool. Significant differences between samples within habitats and weeks (post–ANOVA Tukey tests, $\alpha = 0.05$) are indicated by letters above each column; ns = not significant. ANOVA results are given in Supplementary Information, Table S5.
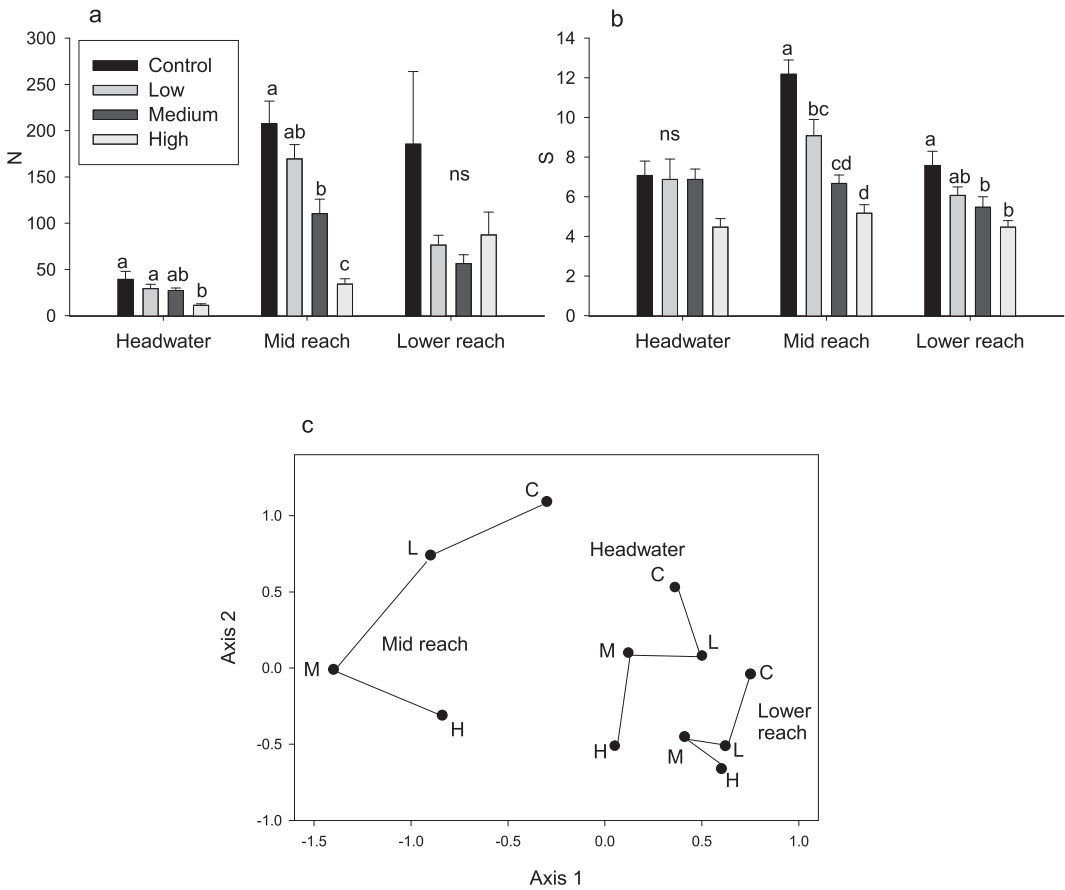
**Figure 4.** Effects of 4 disturbance treatments (control, low, medium and high) in riffles in Yuccabine Creek on stone-dwelling macroinvertebrate density (a) and richness (b) in upper, mid and lower reaches of Yuccabine Creek; and ordination of assemblages resulting from each treatment (c). In (a) and (b) significant differences between samples within streams and habitats (post-ANOVA Tukey tests, $\alpha = 0.05$) are indicated by letters above each column; ns = not significant. ANOVA results are given in Supplementary Information, Table S5.

marked stones had moved up to 12 m downstream at Tam Creek, but with little apparent effect on the assemblage except, possibly, a reduction in density on control stones in Creek 115 (Figure 5(d)). Assemblage resilience to disturbance at Birthday Creek was lower than at the other sites, with reductions in both density and richness; in contrast, samples taken immediately following the disturbance in the PNG streams did not differ from the controls except for density at Tam Creek (1993) (Figure 5(a)). However, time to recovery of density and richness was similar (mostly 2–4 d) among streams (Supplementary Information, Table S4). Ordination and MRPP analysis show overlap in assemblages between disturbed and control samples reflecting the rapid recovery times, except at Tam Creek 1994, but even there samples were close by day 14 (Figure 6).

Macroinvertebrate drift significantly increased following the experimental disturbance at Tam and Birthday creeks in total density (respectively, 68- and 32-fold) and richness (8-fold at both sites) and density of most common taxa (Table 4). Thirty-eight taxa were recorded in the drift at Tam Creek, 19 of which were not recorded from the benthos. Seventy taxa were recorded in the drift at Birthday Creek, 27 of which were not present in the benthic samples.

**Table 4.** Macroinvertebrate drift (density m$^{-3}$) in Tam and Birthday creeks, pre- and post-disturbance, including one-way ANOVA results ($F$, $P$; d.f. = 5).

|  | Pre-disturbance | s.e. | Post-disturbance | s.e. | F | P |
|---|---|---|---|---|---|---|
| Tam Creek |  |  |  |  |  |  |
| *Baetis* sp. 3 | 0.472 | 0.079 | 15.028 | 1.282 | 128.4 | 0.0003 |
| *Baetis* sp. 2 | 0.014 | 0.002 | 2.404 | 0.747 | 10.2 | 0.0329 |
| *Baetis* sp. 1 | 0.059 | 0.006 | 5.075 | 0.721 | 48.4 | 0.0022 |
| Chironomidae | 0.025 | 0.002 | 4.247 | 0.668 | 39.9 | 0.0032 |
| *Cheumatopsyche* | 0.015 | 0.003 | 3.926 | 0.588 | 44.2 | 0.0027 |
| Helminthidae (l) sp. 14 | 0.027 | 0.003 | 2.590 | 0.374 | 47.0 | 0.0024 |
| *N* | 0.680 | 0.052 | 46.472 | 5.379 | 72.5 | 0.0010 |
| *S* | 0.028 | 0.005 | 0.235 | 0.017 | 136.5 | 0.0003 |
| Birthday Creek |  |  |  |  |  |  |
| *Simulium* sp. | 0.483 | 0.055 | 17.489 | 5.428 | 9.8 | 0.0351 |
| Hydroptilidae sp. 1a | 0.575 | 0.056 | 9.740 | 2.639 | 12.1 | 0.0255 |
| *Ulmerophlebia* sp. | 0.024 | 0.002 | 0.421 | 0.219 | 3.3 | 0.1441 |
| Chironomidae | 0.122 | 0.028 | 5.793 | 2.694 | 4.4 | 0.1031 |
| Dixidae | 0.065 | 0.017 | 0.858 | 0.060 | 161.7 | 0.0002 |
| *N* | 1.705 | 0.056 | 54.139 | 14.778 | 12.6 | 0.0238 |
| *S* | 0.057 | 0.007 | 0.432 | 0.025 | 208.6 | 0.0001 |

### Resilience across experiments

Resilience increased with decreasing scale of disturbance (Figure 7). There was clear difference between whole stream (flood) samples and the rest (overall $F_{2,12}$ = 12.32, $P$ = 0.0012; Tukey test, $P$ < 0.05), but not between brick samples and whole-riffle disturbance samples, although the majority were separated. In the post-flood samples, resilience was higher in pool than riffle assemblages; following whole-riffle disturbance, resilience overlapped between PNG and AWT streams; and on the bricks, resilience was low at the Yuccabine Creek mid-reach site, and higher at the other Yuccabine Creek sites and Pixies and Birthday creeks, with a maximum in the Birthday Creek riffle but otherwise similarity between pools and riffles. Minimum and
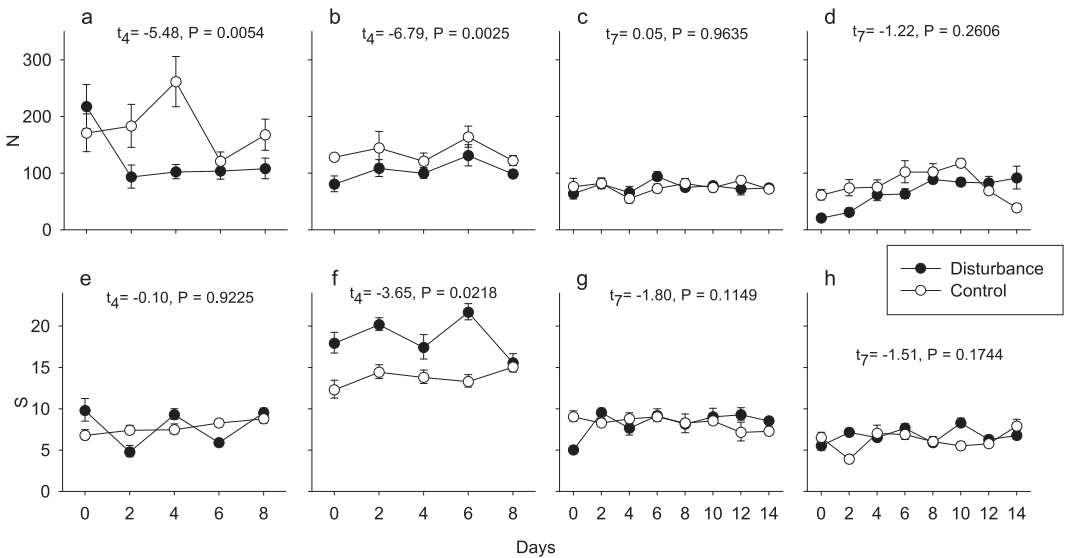


**Figure 5.** Recovery over 8 – 14 d from whole-riffle disturbance by stone-dwelling macroinvertebrates: density (top panels) and richness (bottom panels) in Tam Creek 1993 (a, e), Birthday Creek, 1993 (b, f), Tam Creek, 1994 (c, g) and Creek 115, 1994 (d, h). Comparisons between control and disturbed samples are shown (paired *t* test; *t*, *P*).
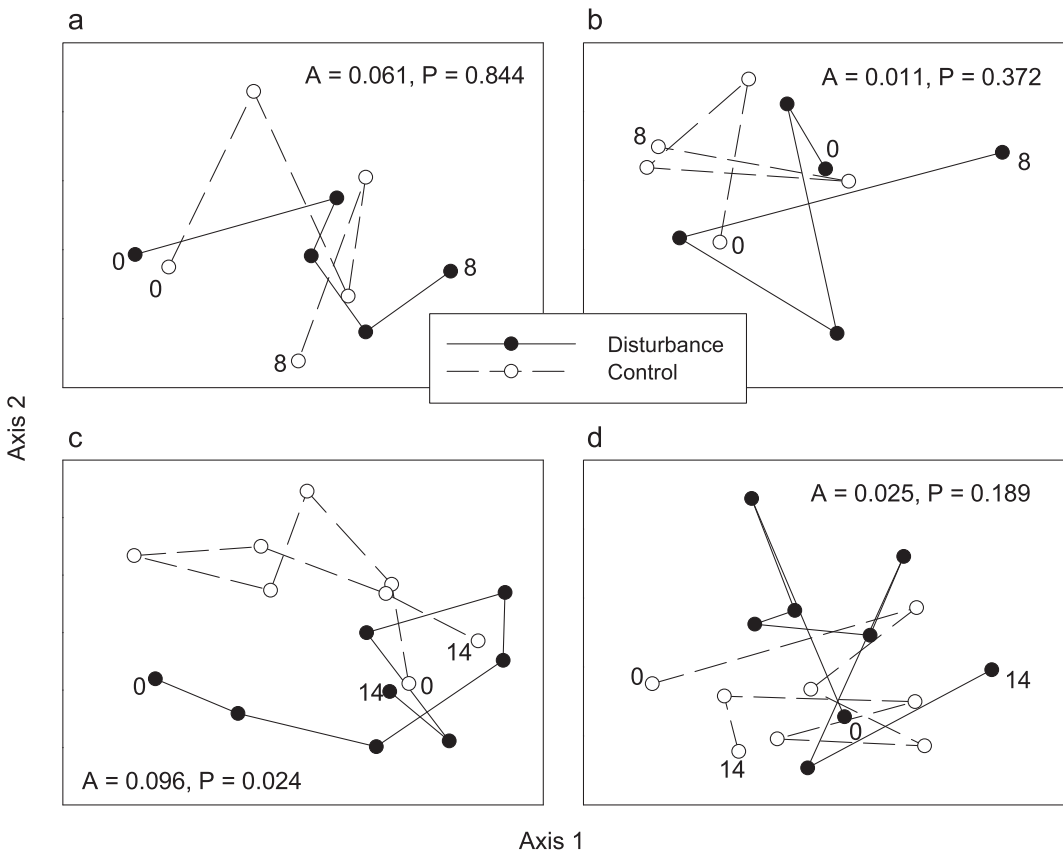
**Figure 6.** Ordinations showing macroinvertebrate assemblage recovery at Tam Creek 1993 (a), Birthday Creek, 1993 (b), Tam Creek, 1994 (c) and Creek 115, 1994 (d). Start and finish samples (0 and 8 or 14 d) are identified. Results of multi-response permutation procedures (MRPP) comparing treatment and control samples (A, P) are shown.

maximum values were both at Birthday Creek, in the post-flood and single-brick samples, respectively.

## Discussion

### *Flood disturbance (macrohabitat – Birthday Creek)*

Our prediction 1, that pools would provide a disturbance refuge, was supported as they accumulated fauna, as elsewhere (Benson and Pearson 1987a; Palmer et al. 1996; Bruno et al. 2016). Prediction 2, that recovery would not be rapid at the whole-stream scale, was partly supported. The apparent recovery period of about 40–45 d in the riffle following the larger flood in Birthday Creek was similar to that in the Yuccabine Creek middle reach (Pearson 2014), greater than for desert streams in the USA (Grimm and Fisher 1989; ~14 days) and intermittent streams in Australia (Boulton and Lake 1992, ~14 d), similar to that recorded for headwater streams in the USA (Angradi 1997, 42 d), less than for streams in New Zealand lowlands (Scrimgeour et al. 1988, 135 d) and Mexican uplands (Molles 1985, 365 d), and much less than for 'catastrophic' floods in Ireland (Woodward et al. 2015, up to 10 years). Recovery in the Birthday Creek pool over 6 to 21 days was at the lower end of this range, and similar to recovery recorded previously in BC riffles (Rosser and Pearson 1995). In the smaller flood (1995), more rapid recovery to pre-flood densities indicated a resilient fauna sourced from flow refugia including pools.
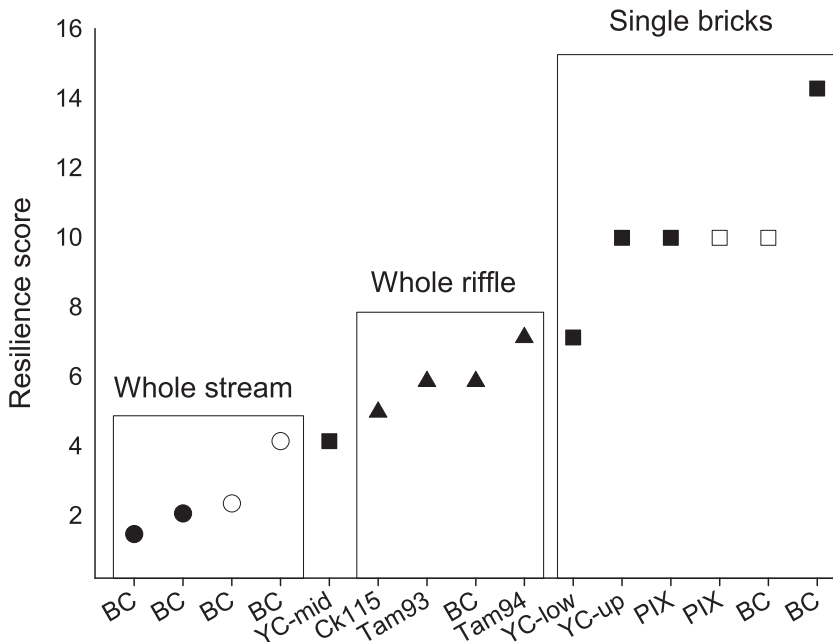
**Figure 7.** Relative resilience of macroinvertebrate assemblages in disturbance experiments at whole-stream (● riffle, ○ pool), whole–riffle (▲) and single–stone (■ riffle, □ pool) scales, with samples ordered by resilience score. Stream abbreviations are BC, Birthday Creek; YC, Yuccabine Creek (upper, middle and lower); Ck115, Creek 115; Tam93, Tam Creek 1993; Tam94, Tam Creek 1994; PIX, Pixies Creek.

### *Experimental microhabitat disturbance – contrasting hydraulics (Birthday, Pixies and Yuccabine Creeks)*

Recovery following disturbance was generally rapid, confirming prediction 3, resulting from small-scale redistribution of nearby colonists, as would occur when patches of the streambed are shifted in moderate spates (Townsend and Hildrew 1976; Benson and Pearson 1987a; Pearson and Jones 1987). However, our prediction 4, of lower resilience in less regularly disturbed sites, was not strongly supported. In Yuccabine Creek, richness was highest in the middle reach but resilience was highest at the lower reach, predicted to be more susceptible to natural disturbance, and reflected in the high proportion of taxa with resilience traits, including *Baetis* and *Simulium* (Mackay 1992; Townsend et al. 1997a). Similarly, in Colorado streams, maximum daily increase in discharge and channel stability – not channel slope – determined magnitude of disturbance (Peckarsky et al. 2014). Instability of the substratum did not explain the longitudinal differences in composition at Yuccabine Creek, as assemblages at the upper site were similar to those from the lower site. Further, the response to disturbance was not always consistent within a taxon: thus, *Baetis* sp. was not affected by the high treatment at the lower site, but at upper and mid-reach sites its density declined substantially. Thus, near-bed hydraulics cannot necessarily be used to predict invertebrate habitat suitability (Jowett 2003).

Our prediction 5, that cumulative effects of multiple disturbances would result in a reduced but resilient fauna was partly supported. However, while multiple disturbances maintained a reduced fauna, there was little further impact beyond the initial disturbance, reflecting the resilience (rapid recovery) of the remaining species.

### Experimental mesohabitat disturbance – contrasting hydrology (Birthday and Tam Creeks and Creek 115)

Recovery at the whole-riffle scale in 2–4 days in Birthday Creek and the PNG streams was quicker than is typically recorded for small disturbed areas (e.g. Matthaei et al. 1996). Our prediction 6 that the more frequently disturbed site (Tam Creek, PNG) would have a less diverse fauna than Birthday Creek was supported. Similarly, richness was inversely related to disturbance in some New Zealand streams (Death 1996), but reached maximum richness with intermediate disturbance in others (Townsend et al. 1997b). However, our results did not consistently support the prediction that the fauna of the more frequently disturbed PNG sites would be more resilient (Poff and Ward 1990). Birthday Creek and Tam Creek had similar resilience following the whole-riffle disturbance, even though the aseasonal PNG and seasonal AWT streams differed in natural disturbance frequency and even though the PNG sites had lower richness than Birthday Creek, as reported for the resilient assemblage of an aseasonal stream on Bougainville Island (PNG), in comparison with Yuccabine Creek (Yule and Pearson 1996). Long-term historical exposure to regular disturbance (i.e. the natural flow regime in PNG) imposes strong selective forces on resilience mechanisms and eliminates opportunistic fauna (Death 1996; Lepori and Hjerdt 2006; Thompson and Townsend 2006) thereby constraining richness but enhancing resilience. However, a less rich fauna in PNG may partly relate to biogeographic issues (Dudgeon 1994).

In seasonal streams, assemblage resilience may fluctuate, being low during periods of stable flow, with increasing densities of non-resilient opportunistic species (e.g. chironomids – Pearson 2014), but increasing during high flows in the wet-season, when assemblage composition approaches that of streams with more regular disturbance. Increased frequency of disturbance filtered out species incapable of persisting under these conditions (Lepori and Malmqvist 2009), but relationships are clearly not straightforward.

While benthic movement of macroinvertebrates can be important in their redistribution in streams (Benson and Pearson 1987a; Pearson and Jones 1987), drift is usually the major mechanism of recovery, particularly with increasing frequency and scale of disturbance (Benson and Pearson 1987b; Palmer et al. 1996; Rios-Touma et al. 2012) and was an important movement mechanism in BC and Tam Creek, with background densities similar to those at Yuccabine Creek (Benson and Pearson 1987a), and greatly magnified post-disturbance. In tropical streams, the presence of all life stages of most insect species through the year (e.g. Benson and Pearson 1988; Yule and Pearson 1996) and rapid development times (Benson and Pearson 1988) facilitate recovery (Mackay 1992).

### Resilience and scale in tropical streams

Resistance or resilience mechanisms allow persistence of populations and assemblages under harsh physical conditions (Poff and Ward 1990). These mechanisms typically involve avoidance or rapid recolonisation from unaffected habitat patches (Townsend et al. 1997b). Avoidance may follow cues such as rising water levels or water velocity (Lake 2000). These cues may have occurred in the Birthday Creek floods, but they did not presage the experimental rock rolling or riffle raking, so the rapidity of response to those disturbances is noteworthy. Our small-scale brick experiments underpinned the rapidity with which denuded areas can be repopulated from surrounding undisturbed patches (Townsend and Hildrew 1976; Pearson and Jones 1987; Resh et al. 1988; Bruno et al. 2016). Our results supported our prediction 7 that recovery would be inversely related to scale of disturbance. Response to large-scale flood disturbance relies on wider-ranging dispersal mechanisms and use of refugia (Gjerløv et al. 2003; Pearson 2014), explaining different responses to the natural disturbance and experiments.

Our results confirm similarities in small-scale resilience between tropical and temperate streams, indicating that disturbance selects a sustained fauna that is resilient (or tuned) to the prevailing disturbance regime. However, we found that expected effects of contrasting hydraulics and hydrology

did not always occur, indicating complexity of relationships between faunal responses (resilience) and local diversity and flow regimes. Our observations and experiments across scales underline the need to consider scale, both temporal and spatial, in assessing or comparing resilience in streams (Lepori and Hjerdt 2006).

## Disclosure statement

No financial interest or benefit has arisen from the application of this research.

## Notes on contributors

*Dr Zoe Rosser* is an independent ecological researcher and educator who now lives in Tasmania.

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