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# Benthic algal resilience to frequent wet-season storm flows in low-order streams in the Australian tropical savanna

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**Abstract:** Storm-flow disturbances are frequent during the wet season of Australian tropical savannas. We examined benthic algal resistance and resilience in open-canopy streams in the Daly River watershed. Storm flows occurred every 2 to 3 d at 1<sup>st</sup>- to 4<sup>th</sup>-order sites, with sharp rises and falls and relatively long periods of shallow, low-turbidity base flow. At a 5<sup>th</sup>-order site, storm-flow duration was longer and base flows were deeper and more turbid. We hypothesized that: 1) storm flow would dislodge benthic algal biomass, 2) baseflow biomass would be low, 3) taxon richness would be low, and 4) algal composition would be dominated by resistant algae with prostrate or erect growth forms or by fast growing colonizing algae. Hypothesis 1 was supported. Storm flows dislodged ~93% of epilithic biomass. Support for hypothesis 2 was equivocal. At the 5<sup>th</sup>-order site, sand mobility prevented establishment of benthic algae until seasonal flows receded. At the other sites, epilithon net growth rates were much greater than rates in some temperate streams. Benthic biomass was typical of temperate oligotrophic streams, but maximum biomass was typical of mesotrophic streams. We attributed the relatively rapid growth and high biomass to warm water temperatures (mean = 29°C, maximum = 36°C), high incident light, rapid algal nutrient uptake, loss of grazing invertebrates caused by storm flows, and physical impediments to fish access. Hypothesis 3 was not supported. Mean taxon richness was high because of the occurrence of rare taxa. Hypothesis 4 was not supported. Epilithic algal biomass was dominated by resistant filamentous chlorophytes. Epilithic algal resistance was similar to resistance in higher latitude streams, but resilience was greater. Epilithic algae potentially could supply autochthonous C to the Daly River and other tropical aquatic food webs.

**Key words:** benthic algae, resilience, resistance, disturbance, storm flow, flood, spate, tropics, filamentous algae

Floods, storm flows, and spates are hydrologic disturbances that can shape the structure, function, and biodiversity of lotic ecosystems, and that vary in magnitude, duration, frequency, and predictability across ecosystems (Lake 2000). As much as 99% of benthic algal biomass can be dislodged by these events (Grimm and Fisher 1989) via drag and shear stress forces, abrasion by suspended sediment, and substrate mobility (Larned 2010). The resistance of benthic algae to hydrologic disturbances, a measure of their capacity to withstand a disturbance (Lake 2000), depends on the physical properties of the disturbance and the composition, physiognomy, and physiology of benthic algal assemblages (Biggs and Thomsen 1995, Peterson 1996). The algae that remains after storm flows typically has a patchy heterogeneous distribution (Peterson 1996).

Resilience is the capacity of a system to recover from disturbance (Lake 2000). Benthic algal recovery after storm-flow disturbance occurs via recolonization by immigrant algae and regrowth of resistant algae; can take days (Peterson

and Stevenson 1992), weeks (Fisher et al. 1982), or months (Uehlinger 1991); and may include a succession of assemblages (Grimm and Fisher 1989). Resilience depends on factors that control benthic algae, such as resource availability (nutrients, light), hydraulic conditions, stressors, such as pollutants, and the strength of biotic interactions, such as grazing (Stevenson 1997, Larned 2010).

Resistance and resilience of benthic algae to storm flows have been studied by experimentation and field studies. In most experiments, researchers tested the effect of a single disturbance (but see Peterson and Stevenson 1992) with field manipulations (Peterson et al. 1994, Wellnitz and Rader 2003, Davie et al. 2012) or in experimental channels with simulated spates (Peterson and Stevenson 1992, Francoeur and Biggs 2006). Most field studies have involved tracking responses of benthic algae to storm flows and floods in temperate rivers and streams (Biggs and Close 1989, Grimm and Fisher 1989, Uehlinger et al. 1996, Biggs et al. 1999, Riseng et al. 2004). In subtropical and tropical studies, re-

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searchers have identified the wet season as a period of lower benthic algal biomass compared to other periods because of frequent storms (Mosisch and Bunn 1997, Yang et al. 2009, Kohler et al. 2012, Tsai et al. 2014).

Storm flows influence the growth form of benthic algae. Prostrate and stalked algal species (Schneck and Melo 2012) can be more resistant to storm flows than filamentous and motile growth forms. Passy (2007) identified low- and high-profile diatom guilds that dominate high- and low-current-velocity epilithon, respectively. The interaction between disturbance and productivity shapes the structure of competing species assemblages (Kondoh 2001, Cardinale et al. 2006). Disturbance favors superior colonizers or disturbance-resistant species, and puts superior competitors at a disadvantage by reducing competitive exclusion. Low species richness is predicted under conditions of high disturbance and low productivity (Kondoh 2001). This prediction has been supported experimentally for benthic algae (Cardinale et al. 2006). In a survey of New Zealand streams, richness was highest when disturbance was low to intermediate and periphyton had high P content, and declined with flood magnitude in streams with unarmored sediments (Biggs and Smith 2002).

Food webs of 1<sup>st</sup>- to 4<sup>th</sup>-order tropical streams are based primarily on autochthonous algal sources, even in moderately shaded forested watersheds (March and Pringle 2003, Mantel et al. 2004, Brito et al. 2006, Moulton 2006, Dudgeon et al. 2010). However, most studies have been conducted during periods of low storm-flow disturbance (i.e., dry season) when benthic algae can accumulate (but see Brito et al. 2006). Reduction of benthic algal biomass by storm flows may decrease the importance of autochthonous C in the wet-season food web.

We examined the resistance and resilience of benthic algae to storm flow during the wet season in 1<sup>st</sup>- to 5<sup>th</sup>-order tropical savannah streams in northern Australia. Storm-flow disturbances are likely to be more frequent and of greater magnitude in the tropics than in temperate climates because of the higher rainfall of many tropical regions (Lewis 2008). Rainfall is more intense in the Australian wet/dry tropics than in many other tropical regions with similar monthly rainfall totals (Jackson 1988). The higher rainfall intensities are more likely to produce hydrographs with sharp rises and falls and to have greater disturbance effect. We hypothesized that frequent storm flows would: 1) dislodge benthic algal biomass, and produce 2) low baseflow biomass, 3) low species richness, and 4) algal assemblages dominated by resistant algae with prostrate or erect growth forms or by fast growing colonizing algae. These effects could be mitigated by adaptation of algae to the frequent storm flows characteristic of the Australian wet/dry tropics and other tropical regions, warm water temperatures that favor rapid algal growth, and high rates of solar radiation typical of the tropics.

## METHODS

### Study area and sites

We worked in the Cullen River watershed and its sub-watershed, Bonrook Creek (Fig. 1), which have a climate and vegetation typical of the uplands of the Australian wet/dry tropics. Monsoonal depressions, cyclonic weather, and convective storms produce a 3- to 4-mo period of high-intensity rainfall over the wet season. At the Pine Creek meteorological station, 3 km north of the Bonrook study area (Fig. 1), 92% of the average total annual rainfall (1141 mm)

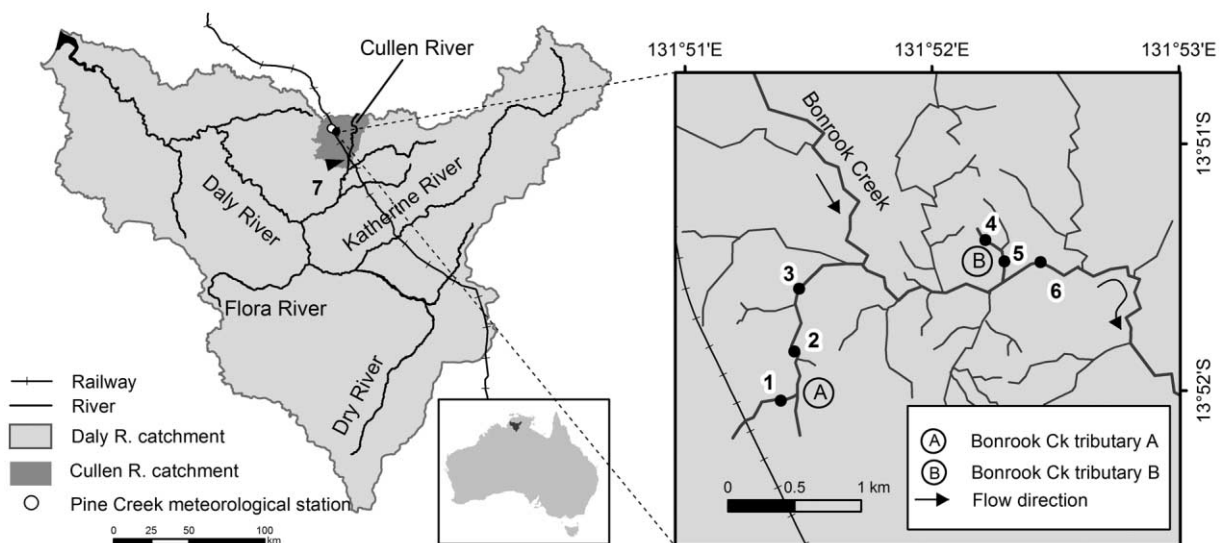


Figure 1. Study sites in the Cullen River and Bonrook Creek watersheds in the upper reaches of the Daly River watershed in the Australian wet/dry tropics.

falls between December and March. This pattern produces a predictable seasonal flow regime over the wet season that extends into the early dry season for the higher-order Cullen River. For most of the year, the Cullen River and its tributaries are dry with few permanent pools.

The Cullen River watershed is hilly, underlain by sandstone and shale, and generally has shallow, infertile soils. The watershed is largely undeveloped, and <1% of the native vegetation has been cleared for land uses, such as roads, a railway corridor, buildings, horticulture, and paddocks. Land use is predominantly low-intensity cattle grazing, but the Bonrook study area is in a sanctuary for wild horses and has no cattle. Vegetation is predominantly eucalypt woodland savannah that extends to the stream and river banks. First-order streams in the Bonrook subwatershed have no riparian plant species, and only the small tree *Pandanus spiralis* is present on the banks of 2<sup>nd</sup>-order streams. *Pandanus spiralis*, *Melaleuca* spp. (paperbark trees), and woodland trees (e.g., *Acacia* spp.) line 4<sup>th</sup>-order Bonrook Creek. Riparian plant species are most abundant on the banks of pools that persist into the dry season after flow has ceased. Canopy cover over Bonrook Creek sites was ~15%, similar to the watershed's terrestrial canopy cover (Table S1). *Melaleuca* trees overhanging the Cullen River produced higher canopy cover (~25%).

### Water and benthic sample collection and analysis

Between November 2008 and May 2009, data were collected from 7 sites (Fig. 1) ranging from 1<sup>st</sup>- to 5<sup>th</sup>-order streams (Table S1). The stream beds were dominated by pebbles, cobbles, and gravel, except at sites 2 and 7 where

sand was dominant. Water and benthic samples were collected approximately every 2 wk (Table 1) between 31 December 2008 and 25 March 2009 from Bonrook sites during base flow, and additional benthic samples were collected at site 6 in mid-February after a storm. At the Cullen River site, water samples were collected until 7 May, but sampling did not begin until 24 March because high flows made sampling unsafe.

Water samples for chemical analyses were filtered through 0.45- $\mu\text{m}$  membranes in the field and stored frozen until analysis for  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and  $\text{NO}_2^-$ , and filterable reactive P (FRP) by standard methods (APHA 1998). The methods were the phenate colorimetric method for  $\text{NH}_4\text{-N}$  (method 4500 D), automated Cd method for  $\text{NO}_3\text{-N}$  and  $\text{NO}_2\text{-N}$  (method 4500- $\text{NO}_3^-$  F), and the automated ascorbic acid reduction method for FRP (method 4500-P F). Each method has a detection limit of 1  $\mu\text{g/L}$ .

Water samples for chlorophyll *a* analyses were kept on ice in the field and filtered through Whatman GF/C glass-fiber filters (Maidstone, UK). Filters were placed in 25-mL glass bottles and frozen within a few hours of collection. In the laboratory, 90% acetone was added to the bottles, and they were refrigerated for  $\geq 12$  h in the dark to extract chlorophyll, which was measured by fluorometry with a non-acidification technique (Welschmeyer 1994) with a Trilogy<sup>®</sup> fluorometer (Turner Designs, Sunnyvale, California). Preliminary trials showed that this time was sufficient to extract chlorophyll from algal cells damaged by freezing. Ultrasonication did not increase dissolved chlorophyll content of the acetone solution.

Five epilithic chlorophyll samples were collected randomly along 25-m reaches at 1<sup>st</sup>-order sites 1 and 4, along

Table 1. In-situ data and sample collection (see Fig. 1 for site locations). PAR = photosynthetically active radiation, chl = chlorophyll.

Site	Description	Hydraulic habitat	Water quality <sup>a</sup>	Epilithic chl and algae	Epipsammic chl	Continuous depth, flow	Continuous temperature, turbidity <sup>d</sup>	Intermittent depth, temperature, turbidity <sup>e</sup>	PAR, turbidity <sup>f</sup>
1	Tributary A	Riffle	X	X					
2	Tributary A	Pool	X		X				X
3	Tributary A	Riffle	X	X				X	
4	Tributary B	Riffle	X	X					
5	Tributary B	Riffle	X					X	
6	Bonrook Creek	Riffle	X	X		X <sup>b</sup>	X		
7	Cullen River	Run	X		X	X <sup>c</sup>		X	X

<sup>a</sup> Biweekly measurements of temperature, conductivity, and pH with a Quanta (Hach Hydromet, Loveland, Colorado) multiparameter probe, and surface turbidity with a Hach Hydromet meter (model 2100P)

<sup>b</sup> Data collected every 10 min (Micro-Diver DI601; Van Walt Ltd., Surrey UK) between 13 November and 7 April; depth corrected for atmospheric pressure; flow calculated from a linear regression of gauged flows and depth ( $r^2 = 0.97$ ,  $p = 0.014$ ,  $n = 5$ )

<sup>c</sup> Supplied by the Department of Land Resource Management for hydrographic station GS8140067

<sup>d</sup> Data collected every 10 min by a Hydrolab DataSonde 4a (Hach Hydromet, Loveland, Colorado)

<sup>e</sup> Periods of up to 2 wk of data collection, every 10 min by a Hydrolab DataSonde 4a

<sup>f</sup> PAR measured at 10-cm depth intervals with a Li-Cor 188B submersible scalar bulb (Li-Cor, Lincoln, Nebraska) and turbidity measured at a depth of 5 cm below the surface with a Hach Hydromet meter (model 2100P)



a 50-m reach at 2<sup>nd</sup>-order site 3, and 100-m reach at 4<sup>th</sup>-order site 6 with a periphyton sampler (Davies and Gee 1993) that scoured an 8.04-cm<sup>2</sup> area with a Velcro™ disk attached to a wooden stick. Each disk was placed in a glass bottle and kept on ice until it was frozen several hours later. Chlorophyll was analyzed as described above. Epipsammic chlorophyll samples were collected by pressing an inverted 44-mm-diameter Petri dish into the substrate and sliding a steel spatula under the lid. The Petri dish was sealed with a lid and electrical tape, kept cold in the field, and then frozen. The contents of the Petri dish were transferred to a glass bottle, acetone was added, and the supernatant was analyzed as described above. Macroalgal % cover (10% increments) was assessed visually at the waterline and to a depth of 0.1 m along a 0.5-m stretch of each bank adjacent to the benthic sampling points at sites 1, 3, 4, and 6.

Two composite benthic samples composed of 5 subsamples were taken from the same sites as the epilithic chlorophyll samples. One sample was preserved in Lugol's iodine for algal identification and enumeration, and the other was preserved in ethanol for diatom identification. Samples preserved in Lugol's iodine were examined in a Lund cell under 400× magnification on a Zeiss Axioskop microscope (Carl Zeiss, Göttingen, Germany) following the method of Hötzel and Croome (1999). Most algae were identified to species, but many genera were represented by a single individual, which prevented the need for further taxonomic identification. *Oedogonium* was enumerated at the genus level, but identification to species level was made on a subset of samples. Taxonomic identification of diatoms was undertaken by treating samples with dilute HCl and H<sub>2</sub>O<sub>2</sub>. Diatom frustules were mounted on slides and viewed with a differential phase contrast microscope at 1500× magnification with immersion oil (Townsend and Gell 2005).

Forty transects across the Lund cell were examined to ensure that ≥150 algal units (individuals, filaments, or colonies) of the 5 most frequently occurring taxa were counted to yield a counting precision of ±16% or better for these taxa. The total number of algal units was >700/sample. Cells in filaments and colonies also were counted. The dimensions of each taxon in a sample were measured and standard geometric formulae were applied to calculate biovolume and cell surface area. Ten cells of each of the 5 most-frequent taxa were measured in each sample and averaged. For less frequent taxa, 1 to 5 cells were measured depending on the taxon's abundance. The total biovolume for each taxon was calculated as the product of its cell concentration and biovolume.

### In-situ data collection

Daily rainfall and irradiance data at station 14933 in Pine Creek Township were provided by the Australian Bureau of Meteorology (Fig. 1). Irradiance was calculated as solar exposure at ground level. These data were derived

from a model based on images taken by the MTSAT-2 meteorological satellite in the visible and near-infrared spectra and integrated over the day. Incident photosynthetically active radiation (PAR) was monitored with a LiCor Li190 Quantum Sensor (Lincoln, Nebraska) in an open area close to site 1 between 11 December and 31 March. Periods of no data collection for up to 2 wk occurred because of damage caused when small marsupials chewed through the equipment's electrical wires.

Continuous or intermittently continuous data were collected at 2<sup>nd</sup>-, 4<sup>th</sup>-, and 5<sup>th</sup>-order streams (see Table 1 for methods). PAR profiles were measured at the 2 deepest sites (Table 1), and attenuation coefficients were calculated as the slope of the regression of depth (independent variable) and ln(PAR). This value was expressed as the euphotic depth, to which 1% of PAR immediately below the surface penetrated the water column.

### Data analyses

**Flow data** Hydrographs were analyzed by classifying periods of base flow and storm flow. Base flow consists of the continuous contribution made by groundwater to stream flow (Gordon et al. 2006). During periods between storms, stream flow is composed of base flow, whereas during storm flows, stream flow is composed of base flow and surface rainfall runoff (quick flow). In our paper, storm flow refers to the total flow during a rainfall-runoff event. Several methods can be used to separate base flow from total stream flow (e.g., Nathan and McMahon 1990), but these methods are not designed to identify the onset and cessation of a storm-flow event. The onset of storm flow is readily identified as a discrete point in time, and was identified as a sharp rise in the depth hydrograph. However, its cessation occurs as a transition from surface-runoff to groundwater-dominated flow. Our use of flow data was descriptive and comparative, so the cessation of storm flow was defined as the time at which the rate of decline of the depth hydrograph decreased to <1 cm every 10 min unless interrupted by another storm-flow event. Trials using other rates of decline (1 cm every 5 or 20 min) did not change the relative differences between sites. Depth was used instead of flow to provide consistency among sites because flow data were not available for the 2<sup>nd</sup>-order stream hydrographs. Declines in depth are not equivalent to flow reductions between sites because flow reduction depends on stream cross-sectional area and current speed. However, our approach produced reasonable descriptive statistics that could be compared because site width increased with stream order (Table S1). The average turbidity for each storm and baseflow period was volume-weighted at sites 6 and 7 and depth weighted at 2<sup>nd</sup>-order sites.

**Nutrients and light** Regression and statistical analyses were done with SigmaPlot software (version 11; Systat Soft-

ware, Chicago, Illinois). When nutrient concentrations were less than the detection limit, a value equal to ½ the detection limit was assigned.  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ , and FRP data did not meet the assumption of normality even after transformation. Therefore, Kruskal–Wallis tests on ranks were used to compare these nutrients among sites, and were followed by Dunn’s pairwise tests when the Kruskal–Wallis tests were significant. A Pearson correlation analysis was used to test for a potential relationship between  $\text{NO}_3^- + \text{NO}_2^-$  and  $\text{NH}_4^+$  concentrations. The relationship between turbidity and euphotic depth was described with a linear regression analysis of combined data from sites 2 and 7.

**Chlorophyll and algae data** The response of benthic chlorophyll to storm flows was analyzed with multiple stepwise regression analysis between median benthic chlorophyll and time since the previous storm peak, the duration of the previous storm, the rate of water-level rise, and storm peak flow at site 6 for each sampling date.

Multivariate analyses of algal assemblages were done with PRIMER (version 6.1.12; PRIMER-E, Plymouth, UK; Clarke and Gorley 2006) on  $\sqrt{(x)}$ -transformed biovolume relative abundance data. A nonmetric multidimensional scaling (NMDS) ordination was done on Bray–Curtis similarity matrices to visualize algal assemblage similarity among sites and sampling dates. Analyses of similarity (ANOSIM) were used to test similarity of assemblages between January and February and among sites when samples were collected on the same dates. Similarity percentage (SIMPER) analysis was used to examine the dissimilarities in assemblages among sites. Species richness and Pielou’s evenness index were computed for each sample. Two-factor analyses of variance (ANOVAs) without replication were used to compare richness and evenness among sites and sampling dates.

## RESULTS

### Storm flows

Total rainfall between 1 December 2008 and 30 April 2009 was 1294 mm, 30% higher than the 124-y long-term average. Rain fell on ½ of the days between December and March and twice in April. Flow in the Bonrook subwatershed and the Cullen River commenced on 19 December after an 88-mm rainfall event at Pine Creek Township.

Seasonal hydrographs varied with stream order and had different periods of continuous and intermittent flow. Cullen River flowed throughout the wet season until mid-May with no periods of intermittent flow, although flow decreased to a small stream ( $<1 \text{ m}^3/\text{s}$ ) within the wide sandy bed twice in December. Flow was initially intermittent in the Bonrook subwatershed and ceased on 3 occasions for periods of up to 3 d between 19 December and 30 December, but the stream bed did not dry. Bonrook Creek and

most tributary inputs continued to flow until March 29. Between storm flows, headwater streams sometimes decreased to a trickle ( $<0.1 \text{ L/s}$ ) flowing between pebbles and cobbles to become a series of disconnected shallow pools often  $<10 \text{ cm}$  deep.

Storm-flow hydrographs also varied with stream order (Table S2). The number of storm-flow events decreased with increasing stream order because events coalesced from  $\sim 35$  at 2<sup>nd</sup>-order sites to 28 at the 4<sup>th</sup>-order site, and to 15 at the 5<sup>th</sup>-order site. Depth, flow, and volume increased with stream order, and the shape of the hydrographs became more attenuated and less flashy (Fig. 2A, C, E, Table S2). Base flow made up  $\sim 95\%$  of flow duration at the 2<sup>nd</sup>- and 4<sup>th</sup>-order sites and 44% of flow duration at 5<sup>th</sup>-order Cullen River.

### Incident light and water quality

Solar radiation was high throughout the wet season (Fig. S1A) and averaged  $22.3 \text{ MJ/m}^2$  during January and February with few days of heavy cloud cover. PAR was correlated with solar exposure ( $n = 50$ ,  $r = 0.84$ ,  $p < 0.001$ ), and averaged  $1584 \pm 73 \mu\text{E m}^{-2} \text{ s}^{-1}$  ( $n = 28$ ) during the 2 h before and after solar noon in January and February.

Turbidity mirrored seasonal hydrographs (Fig. 2B, D, F). Base- and storm-flow turbidity at each site averaged 14 to 47 and 41 to 100 NTU, respectively (Table S2), and tended to increase with stream size. Turbidity reduced the euphotic depth in accordance with the exponential regression:  $z_{\text{eu}} = (4.62 \pm 0.46)e^{-(0.0508 \pm 0.0086)T}$  ( $r^2 = 0.94$ ,  $p = 0.001$ ,  $n = 6$ ), where  $z_{\text{eu}}$  is the euphotic depth (m) and  $T$  is turbidity (NTU). Baseflow PAR at the stream bed of the Bonrook sites was high ( $>200 \mu\text{E m}^{-2} \text{ s}^{-1}$  for a turbidity  $<20$  NTU and depth  $<30 \text{ cm}$ ; Fig. S2) because of high incident PAR characteristic of the low latitude, shallow stream depths, and low turbidity. The Cullen River was  $>1 \text{ m}$  deep with turbidity  $>50$  NTU during the wet season, so PAR was close to  $0 \mu\text{E m}^{-2} \text{ s}^{-1}$  at the river bed (Fig. S2).

Water temperatures were warm ( $23.8\text{--}36.8^\circ\text{C}$ ) and averaged  $29.5 \pm 0.020^\circ\text{C}$  and  $28.2 \pm 0.076^\circ\text{C}$  for base and storm flows, respectively, at site 6. Baseflow diurnal temperature ranges were  $1.5$  to  $7.8^\circ\text{C}$  and were highest in the lower-order streams. Storm flow reduced stream water temperature by as much as  $5^\circ\text{C}$ , and when coincident with overnight minimum temperatures, increased the diurnal range to as much as  $12^\circ\text{C}$ . Conductivity and pH were 10 to  $49 \mu\text{S/cm}^2$  and 5.4 to 6.8, respectively, and were lowest during storm flows.

Overall, soluble N and P concentrations were low, with positively skewed asymmetric distributions (Table 2). FRP and  $\text{NH}_4^+$  concentrations were similar among sites.  $\text{NO}_3^- + \text{NO}_2^-$  also was similar among sites except site 4, which had a median ( $36 \mu\text{g/L}$ ) that was  $10\times$  higher than medians at other sites. However, high  $\text{NO}_3^- + \text{NO}_2^-$  concentrations occurred at all sites, were most frequent early in the wet

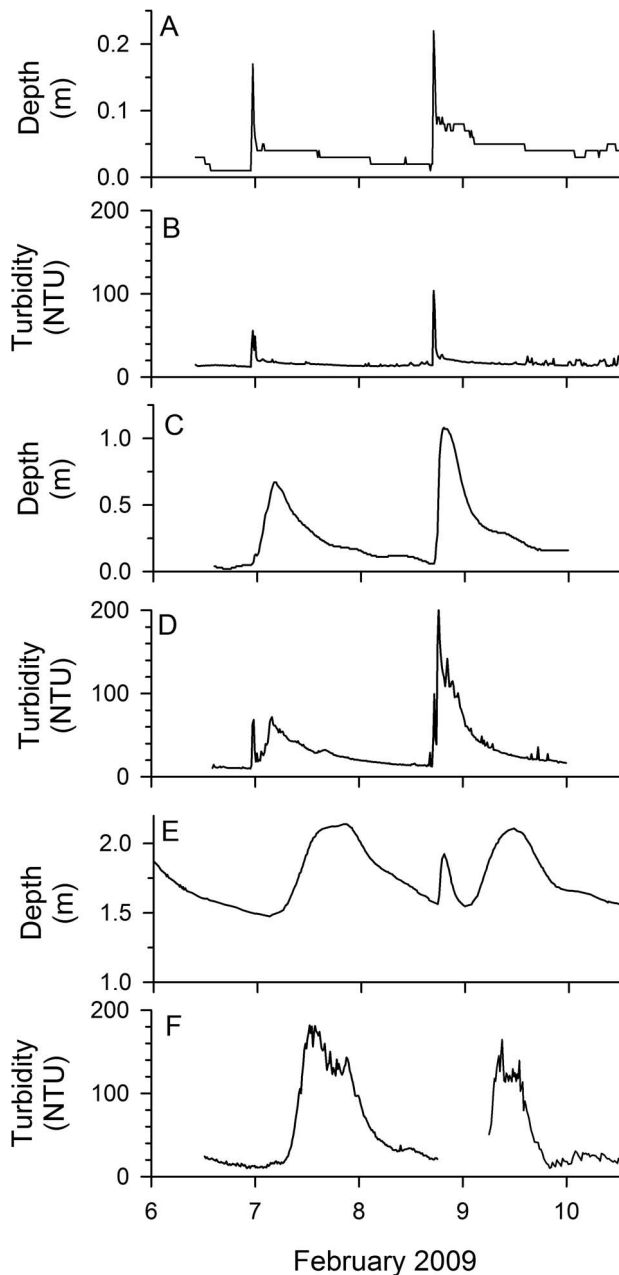


Figure 2. Hydrographs and turbidity for 2 storm flows at 2<sup>nd</sup>-order site 3 (A, B), 4<sup>th</sup>-order Bonrook Creek site 6 (C, D), and 5<sup>th</sup>-order Cullen River site 7 (E, F).

season, and were poorly correlated with  $\text{NH}_4^+$  concentrations ( $n = 26$ ,  $r = 0.37$ ,  $p = 0.063$ ). Soluble N:P molar ratios also exhibited a wide range, mainly because of the wide range of soluble N concentrations (Table 2).

#### Benthic algal resistance and resilience

Substantial amounts of benthic algae persisted through the wet season in the Bonrook watershed (Fig. 3A, B). The median epilithic biomass was 7.9 mg chlorophyll (chl)/m<sup>2</sup>

with a range from <0.1 to 140 mg chl/m<sup>2</sup>. Median epipsammic biomass at the Bonrook Creek pool site (6.5 mg chl/m<sup>2</sup>) was marginally lower than median epilithic biomass, but maximum epipsammic biomass at this site was substantially lower (14.3 chl/m<sup>2</sup>) than maximum epilithic biomass. Median epipsammic biomass at the Cullen River site was 0.3 mg chl/m<sup>2</sup> on 24 March when the sandy substrate was mobile, but was 8.4 mg chl/m<sup>2</sup> during April and May.

Macroalgae were attached to stream banks in the Bonrook watershed throughout the wet season (% coverage <1–80%). Bank algae were most prominent in 2<sup>nd</sup>-order tributaries during the period of base flow in March. A belt of desiccated algae formed as the water level receded. Water-column chlorophyll averaged  $1.2 \pm 0.19 \mu\text{g chl/L}$  in the Bonrook watershed and  $0.31 \pm 0.052 \mu\text{g chl/L}$  in the Cullen River.

Benthic algal resistance to disturbance by storm flow can be assessed by comparing biomass before and after an event (Grimm and Fisher 1989). In mid-February, algal biomass at site 6 decreased from a median of 30 mg chl/m<sup>2</sup> 16 h before a storm-flow event (0.78 m depth, 0.9 m<sup>3</sup>/s) to 2.2 mg chl/m<sup>2</sup> 9 h after the event (93% reduction; arrow in Fig. 3A). After the storm-flow event, the distribution of algal biomass was patchy (range: 0.8–5.4 mg chl/m<sup>2</sup>).

During January and February, biomass ( $b$ ) at site 6 increased linearly with the time ( $t$ ) since the previous storm-flow peak ( $b = [10.4 \pm 0.9]t - [2.1 \pm 3.7]$ ;  $n = 5$ ,  $r^2 = 0.86$ ,  $p = 0.022$ ). However, when March data were included in the analysis ( $t = 10.6$  and 12.6 d), no relationship was found between biomass and flow-related variables, suggesting the period of linear increase of biomass with time did not extend beyond 3.2 d (the median time since the previous storm-flow peak in the January–February data set). Extrapolation of the regression to  $t = 0$  suggests that a median of 2 mg chl/m<sup>2</sup> is resistant to storm flow, but a wide range of biomass is probable. The regression analysis did not take into account variability resulting from disturbance history

Table 2. Nutrient concentrations at Bonrook watershed sites, 31 December 2008–25 March 2009.

Percentile	$\text{NO}_3^- + \text{NO}_2^-$ ( $\mu\text{g/L}$ )	$\text{NH}_4^+$ ( $\mu\text{g/L}$ )	Filterable reactive P ( $\mu\text{g/L}$ )	Molar N:P
Maximum	112	45	25	212
90 <sup>th</sup>	30	35	6	102
75 <sup>th</sup>	7	8	3	37
Median	3	2	3	16
25 <sup>th</sup>	3	1	1	4.7
10 <sup>th</sup>	<1	<1	<1	2.3
Minimum	<1	<1	<1	1.1
$n$	60	25	60	25

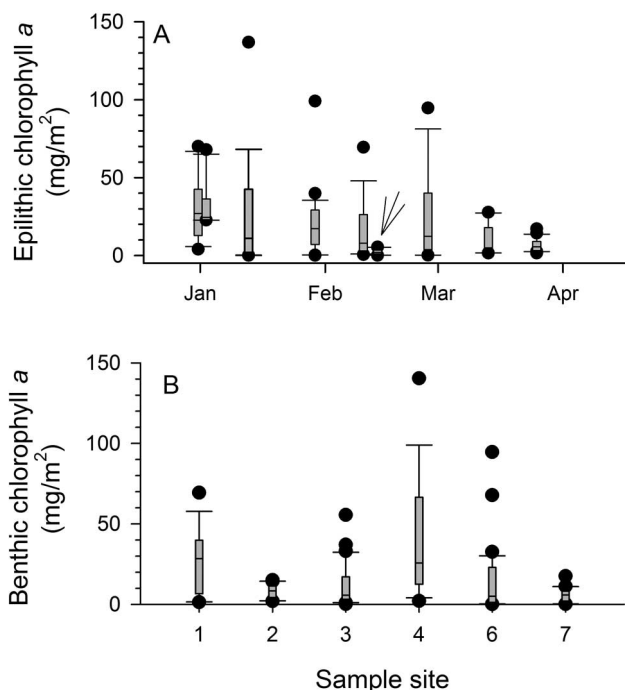


Figure 3. Box plots of collated benthic algal biomass for each sampling date (A) and site (B) during the 2009 wet season. Epilithon was sampled at sites 1, 3, 4, and 6, and epipsammion at sites 2 and 7. No benthic samples were collected at site 5. The 11 February box plot (arrow in panel A) is displaced 3 d for clarity. See Fig. 1 and Table S1 for site descriptions. Benthic biomass at site 7 is for the period 24 March to 7 May. The box plots show 5<sup>th</sup>, 25<sup>th</sup>, 50<sup>th</sup>, 75<sup>th</sup> and 95<sup>th</sup> percentiles, and outliers.

and benthic biomass before the storm event (see Peterson 1996). The regression slope of  $10 \text{ mg chl m}^{-2} \text{ d}^{-1}$  equates to the rate of net biomass accrual after a storm-flow event, and constitutes a measure of algal resilience to storm flow.

### Bonrook watershed epilithic algae

A total of 146 taxa were identified from 16 samples (Table S3). Taxa comprised 55 chlorophytes, of which almost  $\frac{1}{2}$  were desmids, 65 diatoms, and 17 Cyanoprokaryota. The taxon frequency distribution approximated a log-normal distribution, typical of most natural distributions (Preston 1948), with few common taxa and many uncommon or rare taxa (Table S3). Sample taxon richness and evenness averaged  $34 \pm 4.4$  and  $0.40 \pm 0.12$ , respectively, at the Bonrook sites. Neither sample richness nor evenness differed among sites or sampling dates, but total richness was higher at the 4<sup>th</sup>-order site (123 taxa) than at the upstream sites (33–59 taxa).

Insight into the effect of storm flow on species richness can be gained by comparing assemblages before and after

the mid-February storm-flow event when biomass decreased 93%. Species richness before (61 taxa) and after (61 taxa) the event did not differ. Forty of these taxa were common and 21 taxa were either dislodged or recent immigrants. The 6 most common taxa based on biovolume (*Oedogonium*, *Cryptomonas*, *Zygnema*, *Mougeotia*, *Gloetrichia*, *Spirogyra*) retained their relative ranking and total relative biovolume abundance (63%). The most common taxa based on cell numbers (*Aphanocapsa*, an unidentified small spherical chlorophyte, *Cryptomonas*, *Oedogonium*, *Gomphonema affine*) also retained their ranking, with relative abundances for these taxa totaling 87% before and 74% after the storm-flow event. Most taxa absent (22) or new (14) after the storm-flow event were rare (relative abundances  $<0.1\%$ ), and may have been present but not observed in pre-storm-flow samples because of their naturally low abundance. NMDS ordination analysis provided further evidence that algal assemblages affected by storm flows were closely related to predisturbance assemblages (Fig. 4).

Filamentous chlorophytes made up a small proportion of cell relative abundance, but dominated epilithic biovolume abundance because of their large cell volumes (Tables 3, S4A, B). Diatom taxa were present in  $\leq 25\%$  of samples (except *Brachysira* spp.; Table S3), and collectively represented a small proportion of the total relative cell (3.9%) and biovolume (0.76%) abundances. Almost  $\frac{1}{2}$  the diatom taxa have been recorded as epiphytic on macroalgae in the region (Townsend and Gell 2005).

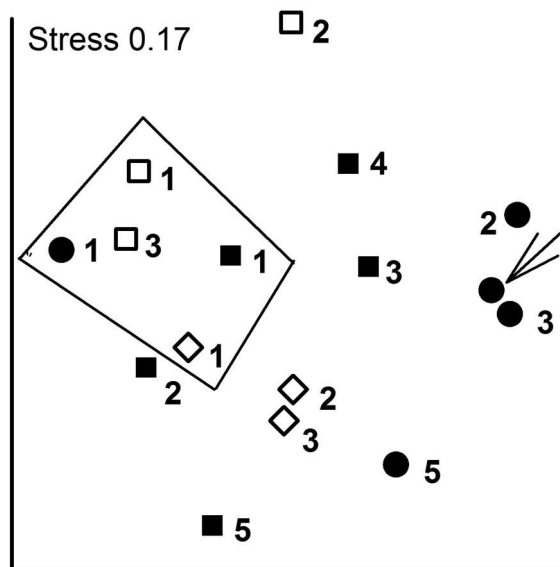
At the beginning of the wet season (13 January) *Oedogonium* was dominant at all sites (27–91% relative abundances), and algal assemblages were similar among sites (Fig. 4). As the season progressed, assemblages tended to follow site-specific temporal trajectories and were characterized by varying proportions of filamentous algae. SIMPER dissimilarity within sites (45–57%) and dates (36–51%) was only slightly lower than dissimilarity between pairs of sites (49–61%) and dates (53–56%) and were attributable mainly to varying relative abundances of *Zygnema* and *Oedogonium*. Despite this variability, assemblages did not differ among dates (ANOSIM, global  $R = 0.27$ ,  $p = 0.08$ ) or sites (ANOSIM, global  $R = -0.074$ ,  $p = 0.66$ ).

## DISCUSSION

### Resistance

The hypothesis that storm flows would dislodge a substantial proportion of benthic algae was supported. The average loss of epilithic biomass in the Bonrook watershed was similar to the upper range reported by Grimm and Fisher (1989) for a desert stream in the southwestern USA who found that algal resistance (% remaining after a storm-flow event) varied with the magnitude of the event. However, in our study, resistance did not vary with storm-flow





### Site legend

- Tributary A, site 1 (1<sup>st</sup> order)
- Tributary A, site 3 (2<sup>nd</sup> order)
- ◇ Tributary B, site 4 (1<sup>st</sup> order)
- Bonrook Ck, site 6 (4<sup>th</sup> order)

### Date legend

- 1 January 13
- 2 January 29
- 3 February 10
- 4 March 13
- 5 March 25

Figure 4. Nonmetric multidimensional scaling ordination plot of Bonrook watershed epilithic biovolume relative abundances. Samples were collected in 2009. The polygon encloses all 13 January assemblages. The arrow points to an assemblage sampled on 11 February several hours after a storm flow.

magnitude, possibly because the disturbance events sampled during the study period did not encompass the full range of storm-flow magnitudes or because a larger data set will be needed to explore this relationship further.

Movement of the sand substrate prevented establishment of benthic algae in the Cullen River during the wet season. Critical current speeds for sand transport (20 cm/s; Allan and Castillo 2007) were exceeded during storm flows and high base flows during most of the 2009 wet season (Department of Land Resource Management, Northern Ter-

ritory, unpublished data). At the pool site in the Bonrook Creek tributary, sand was mobilized during storm flows (and buried a multiparameter probe on one occasion), but was stable during base flows (SAT, personal observation). Moreover, in the Bonrook watershed, aggregations of gravel in the stream bed suggest flows strong enough to mobilize gravel.

The hypothesis that resistant algae would consist of prostrate or stalked taxa was not supported. Resistant algae were primarily filamentous, an unexpected result because filamentous forms are considered less resistant than other forms to storm flows (Grimm and Fisher 1989, Biggs and Thomsen 1995, Schneck and Melo 2012). The persistence of filamentous algae throughout the wet season and the mid-February post-storm data provide strong evidence for the resistance of filamentous chlorophytes. This conclusion is supported by research by Power and Stewart (1987), Cardinale et al. (2006), and Yang et al. (2009). Resistance can decline with assemblage age (Petersen and Stevenson 1992), so the newness of the filamentous assemblages probably reduced dislodgement. Adaptations that enhance tensile strength (e.g., filament twisting) and substrate attachment also may have contributed to resistance.

### Resilience

The hypothesis that benthic algal biomass would be low during the wet season was not supported unequivocally. Benthic algae in the Bonrook subwatershed persisted through the wet season despite a high level of disturbance (every 2–3 d) that removed most biomass. Recovery in Bonrook Creek increased linearly with time, and assemblages attained an average biomass and seston chlorophyll concentration comparable to those of oligotrophic temperate waters, and maximum biomass comparable to mesotrophic conditions (Dodds et al. 1998). Rapid accumulation of algal biomass indicates a high level of resilience in the Bonrook subwatershed, despite the short baseflow period of just a few days between frequent disturbance events.

The open canopy, high insolation, and shallow water in these streams combined to produce warm temperatures (24–37°C), which probably explain the rapid rates of benthic algal accumulation in the Bonrook subwatershed because growth doubles with every 10°C increase in temperature (DeNicola 1996). The rapid growth also suggests that algae had thermal tolerance. Similarly high temperatures have been measured during the wet–dry season transition in the perennial Daly River where *Spirogyra* is dominant (34°C in October; Townsend and Padovan 2005). Net accumulation rates in Bonrook Creek were 2× rates measured in a desert stream (Grimm and Fisher 1989) where summer water temperatures were 20–30°C, and were >1 to 2 orders of magnitude higher than summer and winter ac-

Table 3. Relative abundance of the 10 highest biovolume ranked epilithic taxa in the Bonrook Creek watershed. All taxa have filamentous growth form excluding *Cryptomonas* and *Pyramimonas* which are single cell flagellates.

Taxon	% samples present	% abundance (biovolume)	% abundance, (cells)	Mean cell volume ( $\mu\text{m}^3$ )	Surface : volume ratio
<i>Oedogonium</i> <sup>a</sup>	100	38.8	5.0	2700-6900	0.3
<i>Zygnema</i>	63	18.8	0.8	59000	0.073
<i>Cryptomonas</i>	100	7.9	12.0	180	0.86
<i>Mougeotia</i>	75	7.5	0.4	14000	0.28
<i>Bulbochaeta</i>	25	6.5	1.6	2700	0.44
<i>Gloetrichia</i>	81	5.6	26.1	50	1.0
<i>Spirogyra</i>	50	3.9	0.1	15000	0.27
<i>Trichodesmium</i>	13	3.0	2.7	170	1.1
<i>Pyramimonas</i>	100	0.8	1.1	130	0.94
<i>Teilingia granulata</i>	31	0.8	0.2	2600	0.46
Percentage total		93.5	50.0		

<sup>a</sup> 6 species identified (see Table S3)

cumulation rates, respectively, in New Zealand streams where water temperatures were 4 to 14°C (Francoeur et al. 1999).

Algal recovery depends on availability of nutrient and light resources. The deeper water and higher turbidity of storm flows and some baseflow periods early in the wet season reduced PAR at the stream bed, but these periods constituted a minor part of the wet season (~10% in January and February at site 6), and ½ the storm-flow events occurred at night. PAR at Bonrook stream beds during periods of low-turbidity base flows generally exceeded the photosynthetic saturation rates typical of benthic algae (100–400  $\mu\text{E m}^{-2} \text{s}^{-1}$ ; Hill 1996). However, self-shading within filamentous algal mats (see Binzer et al. 2006) probably limited photosynthetic rates. Storm flows carried high concentrations of suspended sediment (inferred from the high turbidity), but no smothering of benthic algae by silt was observed.

The greater depth and turbidity of the Cullen River, compared with the Bonrook streams, reduced PAR at the river bed approximately to compensation-point rates (10–40  $\mu\text{E m}^{-2} \text{s}^{-1}$ ; Hill 1996), but mobility of sand, the dominant substrate, would have been the overriding factor limiting benthic algal colonization and growth. The Cullen River was unable to support epipsammic primary production until flow, depth, and turbidity declined late in the wet season and substrate stabilized. PAR at the stream bed was controlled indirectly by watershed hydrology and geology (see Stevenson 1997) through depth and turbidity and varied with stream size and position within the drainage network.

In addition to light limitation induced by self-shading, nutrient availability probably constrained algal recovery because it and accrual time account for a large proportion of

variability in riverine algal biomass (Biggs 2000). Baseflow soluble nutrient concentrations generally were low, suggesting high rates of algal uptake to sustain rapid growth rates. The relative requirements for N and P for optimal growth of the dominant filamentous chlorophytes probably exceeded the Redfield N:P molar ratio (16:1) because the optimal N:P for *Spirogyra fluviatilis* in the Daly watershed during the dry season is 87:1 (Townsend et al. 2008). This value seems to be a reasonable basis for comparison given the similar morphology and class-level taxonomic composition of the wet-season chlorophytes. The optimal N:P for filamentous chlorophytes at Bonrook Creek is substantially higher than the Redfield ratio. This ratio and the lower soluble molar N:P ratios (Table 2) suggest that N was the most limiting nutrient, except when soluble N concentrations were high. High soluble N concentrations could have originated from oxidation of atmospheric N by lightning during storms (Noller et al. 1985). The low diatom biovolume abundance was not caused by Si limitation because concentrations in the Bonrook and Cullen watersheds were >3 mg/L (Department of Land Resource Management, Palmerston, Australia, unpublished data), which is greater than the concentration that limits diatom growth (0.5 mg Si/L; Reynolds 2006).

In midwestern American streams, algal biomass depended on nutrient supply when invertebrates were reduced by floods (Riseng et al. 2004). In our study area, storm flows deplete benthic invertebrate abundance and richness in low-order streams (Douglas et al. 2003, Townsend et al. 2012b), which probably reduced invertebrate grazing. However, fish and shrimp (de Souza and Moulton 2005) could have exerted top-down control on benthic algae. Longitudinal connectivity during the wet season permits fish to move into the upper reaches of

the Daly watershed (Warfe et al. 2011). During February 2009, omnivorous (catfish; *Neosilurus hyrtlii*) and algivorous (Bony Bream; *Nematalosa erebi*) fish that could impose a top-down control of benthic algae were collected at the Bonrook Creek site 6 (MD, unpublished data). However, top-down control of algal biomass by fish in Bonrook headwaters, especially 1<sup>st</sup>-order streams, may have been constrained by impediments to fish passage, such as shallow depths of rock bars and riffles, intermittent flow, and lack of pools or deep-water refuges. No fish or shrimp were observed in the 1<sup>st</sup>-order streams during site visits, but tadpoles, which can exert top-down control of benthic algal biomass (Ranvestel et al. 2004), were seen in January.

Benthic algae in the Bonrook watershed was dominated by resistant taxa that recovered quickly and competed successfully for resources rather than species adapted for dispersal and rapid colonization. The composition of post-storm-flow Bonrook algal assemblages resembled their pre-disturbance composition but varied over the wet season. The filamentous algae in Bonrook subwatershed consisted mainly of taxa with large cells, low surface-area: volume (SA:V) (Table 3), and morphology and growth form characteristic of K-strategists (sensu Grime 1979) that compete successfully for nutrients and light resources. Smaller-celled filamentous algae with higher SA:V (e.g., *Gloetrichia*) were a minor proportion of algal biovolume. The most abundant high-SA:V alga was the unicellular flagellate *Cryptomonas*, which usually is pelagic but can be associated with benthic filamentous assemblages (Leland 2000).

Filamentous algae often are dominant in stable lotic environments over a wide range of trophic states (Biggs et al. 1998) and are considered late succession growth forms (Steinman 1996). Like late-successional algae in undisturbed temperate streams (McCormick and Stevenson 1991), filamentous algae in our study system probably exclude other algae via rapid rates of nutrient and CO<sub>2</sub> uptake and a growth form that shades low epiphytic diatoms.

Our study system differs from systems in other studies of disturbance in which diatoms were a more prominent component of the algal assemblage (e.g., Peterson and Stevenson 1992, Biggs 1995). The patterns of resistance and resilience of filamentous chlorophytes in Bonrook Creek and its tributaries mostly closely resembles the patterns reported by Power and Stewart (1987) after a major flood in an Oklahoma (USA) stream. They reported an immediate 2/3 decline in macroscopic filamentous chlorophytes, which regained dominance 25 d later. Resistance and resilience were likely to have been much greater at the microscopic scale; e.g., persistence of basal holdfasts despite loss of overstory filaments. Like Bonrook Creek, the Oklahoma study site was unshaded, had low P concentrations (<3 µg/L), and warm water temperatures (23–36°C). The resistance and resilience of epilithic filamentous chlorophytes to storm flows in streams with low concentrations of growth-limiting nutrients, warm temperatures, and high

incident light extends their distribution to high-disturbance environments in the resource-disturbance–habitat matrix by Biggs et al. (1998).

### Richness

Epilithic taxon richness (11–65) in the Bonrook subwatershed was higher than expected, but comparison of our results with those of others is difficult because of differences in counting methods, geography, and habitat. Bonrook subwatershed richness was higher than the 3 to 27 taxa per sample in New Zealand streams sampled up to 50 d after a flood (Biggs and Smith 2002) and was higher than the 12 to 40 species per sample in the field experiment done by Cardinale et al. (2006). However, Bonrook subwatershed taxon richness (146) was lower than richness during the dry season at a reach in the Daly River (218 taxa; Townsend et al. 2012a) and nearby Edith River (372 taxa; SAT, unpublished data). Richness in the Daly and Edith Rivers was estimated from 1/2 the number of samples used in our study, but with the same sample identification methods. The difference in richness between the wet and dry seasons supports the conjecture by Biggs and Smith (2002) that taxa less resistant to disturbance (slow immigration and growth rates) are able to colonize streams during the less-disturbed dry season, thereby increasing richness. Alternate explanations of higher dry- than wet-season richness include the presence of facultative planktonic–benthic taxa (Townsend et al. 2012c) during the dry season or seasonal differences in other factors, such as water quality, productivity, and immigrant sources.

Total species richness in the Bonrook watershed increased unexpectedly over the period of storm-flow disturbances, whereas evenness did not. The increase in richness was caused by accumulation of rare taxa. This result implies that the pool of taxa or the number of individuals belonging to rare taxa increased over the wet season, thereby increasing the probability of dispersal and colonization. The relatively low number of rare taxa early in the wet season might have been a consequence of the preceding dry season, during which the stream was dry for several months. Another possibility is that rare taxa immigrated from outside the watershed, e.g., via aquatic birds or feral pigs.

The frequent occurrence of rare and uncommon taxa in our data does not lend support to the hypothesis that frequent storm-flow disturbances would lead to low species richness. Rare taxa can be genuinely rare or can be transient taxa that are common in other aquatic environments (Magurran and Henderson 2003). An underlying assumption of the diversity–disturbance hypothesis is competition among taxa adapted to the environment of interest. Thus, transient taxa adapted to other environments are not relevant in tests of the diversity–disturbance hypothesis. The low richness reported by Cardinale et al. (2006) probably was not confounded by the influence of

rare taxa because they examined species richness after 14 to 17 d on artificial substrates that limited immigration of rare taxa.

### Foodweb implications

A growing body of evidence indicates the importance of algal C to tropical-river food webs (e.g., Douglas et al. 2005, Jardine et al. 2012). Low-order streams (1<sup>st</sup>–4<sup>th</sup>) of the Bonrook and other Daly watershed streams constitute at least 95% of the drainage network. C in the higher-order riverine food web may arise from benthic algal production in low-order streams as well as from high-order riverine–floodplain sources (Jardine et al. 2012). However, the potential contribution of low-order streams to the river's wet-season benthic primary production could vary among wet seasons and in response to the duration and frequency of disturbance events. For example, fewer disturbances could extend benthic primary production to higher-order streams, whereas benthic production in 1<sup>st</sup>-order streams could be constrained by intermittent flows caused by lower rainfall and groundwater recharge.

Heavy vegetation in the stream channel and along the banks of perennial headwater streams reduce incident PAR (SAT, unpublished data). Thus, the potential that autochthonous algal production in low-order streams could support the Daly River food web probably is limited to production in open-canopy, seasonally flowing streams (the vast majority of streams in the watershed). However, the high C:N:P (Townsend et al. 2008) and inferred low nutritional value of filamentous chlorophytes in streams dominated by these species may reduce their importance in the food web. Impediments to movement of fish into low-order streams and the probable reduction of invertebrate abundance and grazing by storm flows may further reduce the importance of benthic algae to the riverine food web. It is possible, though, that sloughed headwater algal biomass may support downstream invertebrate filter-feeders. Stable-isotope and other studies are required to estimate the contribution of low-order, especially headwater, primary production to stream food webs.

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