

# Do productivity and disturbance interact to modulate macroinvertebrate diversity in streams?

Jonathan D. Tonkin · Russell G. Death ·  
Kevin J. Collier

Received: 23 January 2012 / Revised: 27 June 2012 / Accepted: 30 July 2012  
© Springer Science+Business Media B.V. 2012

**Abstract** Although disturbance and productivity are clearly strong influences on lotic diversity, rarely have their interactive effects been studied in running water systems. We hypothesised that the presence or absence of canopy cover in streams would alter productivity–disturbance–diversity relationships due to differential effects on the food base, and tested this hypothesis in 47 mountain streams in the central North Island of New Zealand. Canopy cover had no influence on algal biomass in these streams, but a link between disturbance and productivity was found in open canopy

streams where taxonomic richness of invertebrates increased log-linearly with increasing algal biomass and peaked at intermediate levels of disturbance. Community evenness declined with disturbance, but only at closed canopy sites where both invertebrate taxonomic richness and Simpson’s diversity index were higher. Although there was a peak in richness at intermediate rates of disturbance, our results do not directly match predictions of the dynamic equilibrium model which predicts that the level of disturbance maximising diversity interacts with habitat productivity. Rather, we suggest the combined effects of productivity and disturbance are additive rather than multiplicative such that productivity simply sets the upper limit to richness in streams.

Handling editor: David Dudgeon

J. D. Tonkin (✉) · R. G. Death  
Institute of Natural Resources – Ecology (PN-624),  
Massey University, Private Bag 11-222, Palmerston  
North, New Zealand  
e-mail: jdtonkin@gmail.com

*Present Address:*

J. D. Tonkin  
Department of Marine and Environmental Management,  
Bay of Plenty Polytechnic, Private Bag 12001, Tauranga,  
New Zealand

K. J. Collier  
Centre for Biodiversity and Ecology Research,  
Department of Biological Sciences, School of Science and  
Engineering, University of Waikato, Private Bag 3105,  
Hamilton, New Zealand

K. J. Collier  
Waikato Regional Council, P.O. Box 4010, Hamilton  
East, Hamilton, New Zealand

**Keywords** Dynamic equilibrium model · Trade-off · Intermediate disturbance hypothesis · Richness · Canopy cover

## Introduction

Establishing which factors control diversity in nature has long been an important theme of research in ecology (Huston, 1994; Rosenzweig, 1995; Hubbell, 2001). Although many factors can affect diversity, there is still considerable debate over how they might interact (Hubbell, 2001). In particular, several studies in a variety of ecosystems have demonstrated that disturbance and productivity can interact to affect

diversity (Currie, 1991; Wootton, 1998; Mittelbach et al., 2001; Death & Zimmermann, 2005; Cardinale et al., 2006). However, these two factors are often assessed in isolation of each other, and few attempts have been made to assess the interactive effects of productivity and disturbance on diversity in stream communities.

Disturbance is one of the major structuring forces on diversity (Resh et al., 1988; Mackey & Currie, 2001), although the shape of this relationship is highly variable (Mackey & Currie, 2001). In fact, a number of models have been proposed to explain this link, most notably the intermediate disturbance hypothesis (IDH) (Grime, 1973; Connell, 1978; Sousa, 1979). However, while stream communities clearly respond to disturbance (Resh et al., 1988; Lake, 2000; Death, 2010), there has been little empirical support for the IDH in these systems; possibly due to the high mobility of stream organisms compared to the forest communities for which the IDH was originally developed (but see Townsend et al., 1997). In lotic systems, the disturbance–diversity relationship can be confounded by the fact that disturbance not only acts directly on benthic invertebrates but also indirectly by the removal of food resources (Death, 2002). Accordingly, both in lotic communities and in general, the nature of the disturbance–diversity relationship appears to be controlled by habitat productivity altering population growth rates or recolonisation (Huston, 1979; Huston, 1994; Kondoh, 2001; Cardinale et al., 2006).

The relationship between productivity and diversity has also been an important research theme in ecology (Currie, 1991; Abrams, 1995; Mittelbach et al., 2001). However, just as with the disturbance–diversity relationship, the form of the relationship can be highly variable between systems and scales (Abrams, 1995; Mittelbach et al., 2001). The most commonly reported relationships are unimodal (e.g. Huston, 1979; Rosenzweig, 1995; Mittelbach et al., 2001) or linear (e.g. Currie, 1991; Abrams, 1995; Mittelbach et al., 2001) increases in diversity with increasing productivity. The variation in observed patterns may be a result of the scale of observation which has ranged from local, to regional and global comparisons (e.g. Currie, 1991; Chase & Leibold, 2002). Local scale studies often find unimodal relationships (Mittelbach et al., 2001; Chase & Leibold, 2002) which are potentially explained by many mechanisms often related to a competitive-colonising trade-off. However, competition

independent factors such as size differences of individuals with productivity gradients or the geographic extent of high productivity sites may also play a part (Rosenzweig & Abramsky, 1993; Abrams, 1995).

An extension of the IDH, the dynamic equilibrium model (DEM) (Huston, 1979, 1994), predicts that the level of disturbance maximising diversity changes with habitat productivity. Several studies have recently assessed the DEM in a variety of ecosystems (e.g. Scholes et al., 2005; Cardinale et al., 2006; Svensson et al., 2007; Haddad et al., 2008), but the results have been equivocal with the responses of communities to productivity and disturbance differing between ecosystems with little evidence of interactive effects (but see Cardinale et al., 2006). Using the patch occupancy models of Hastings (1980) and Tilman (1994), Kondoh (2001) expanded the DEM to account for metapopulation dynamics, multiple trophic levels and patchy disturbances. This modified model provides an alternative to prior models by allowing disturbances to create niche opportunities for the expression of differing life-history traits.

The presence or absence of canopy cover in small streams can influence the way in which disturbance affects macroinvertebrate diversity by regulating primary productivity (Robinson & Minshall, 1986; Death, 2002; Death & Zimmermann, 2005; Fuller et al., 2008). Post-flood recovery of the food base (periphyton) is likely to be the major determinant of invertebrate diversity in autotrophic streams (Death & Zimmermann, 2005), but this may not be the case in heterotrophic streams if the resource base is relatively unaffected by disturbance (i.e. as much organic matter is washed in as is washed out). In fact, the resistance and resilience of stream communities to flood events is likely to differ with canopy presence or absence through the effects of disturbances on the resource base (Fuller et al., 2008). Complex responses of macroinvertebrate communities to the interaction of productivity and disturbance between heterotrophic and autotrophic streams pose challenges to the generalised application of models such as the DEM.

In this study we evaluate the DEM using benthic macroinvertebrate communities from mountain streams in the central North Island of New Zealand. We investigate whether the observed levels of productivity and disturbance are sufficient to explain diversity patterns in these streams, or whether the relationship is modulated by the presence of canopy

cover over the stream. We hypothesise that benthic invertebrate diversity is a product of the interaction between substrate disturbance and primary productivity, assessed as bed stability and periphyton biomass, respectively. Specifically, diversity will be an increasing function of the interaction between disturbance and productivity. Moreover, we predict that the fit of this relationship will be stronger at open canopy sites than at sites with canopy due to tighter coupling of invertebrates with algal food resources. We discuss whether diversity patterns in these streams can be better explained by a modified productivity–disturbance–diversity model.

## Methods

### Study sites

Forty-seven first- to sixth-order streams and rivers were selected for sampling around the mountains of the Tongariro National Park, central North Island, New Zealand. The park is dominated by the central volcanic massif of Mt Ruapehu (2,797 m asl), Mt Ngauruhoe (2,287 m asl) and Mt Tongariro (1,967 m asl) and the Tihia-kakaramea volcanic massif to the north made up of predominantly andesitic geology. The Kaimanawa Ranges rise to ~1,799 m asl to the east of the Tongariro National Park and are made up of Torlesse Group graywackes and argillites, with variable coverings of volcanic ash deposits. The northern and western parts of the park have an average rainfall of 1,800–3,500 mm year<sup>-1</sup>, with the south and east only receiving around 1,100 mm year<sup>-1</sup> due to the rain-shadow cast by the three mountains from the prevailing westerly winds. Vegetation within and around the park varies from broadleaf-podocarp, mixed beech-podocarp, exotic *Pinus radiata* plantation, native tussock and scrubland, to bare ground in the eastern rain-shadow of the three central volcanoes.

All sampling sites had less than 10% catchment pastoral land use and greater than 90% volcanic hard sedimentary geology. Thus, water quality at these sites is relatively unimpaired by human influences, and flows are unmodified other than the effects of run-of-river hydro-electric dams at ten sites. Elsewhere sites varied hydrologically from stable spring-fed streams, to runoff-fed streams.

### Biological collections

Macroinvertebrates were sampled on one occasion from early February to late April 2007. Five 0.1 m<sup>2</sup> Surber samples (500 µm mesh) were taken from random locations in riffles throughout approximately 50 m reaches at each site. Samples were preserved in 10% formalin and later identified in the laboratory to the lowest possible taxonomic level using available keys (e.g. Towns & Peters, 1996; Winterbourn et al., 2000). Taxa that could not be taken to species level were identified to morphospecies, including some Chironomidae and Oligochaeta. Density (individuals 0.1 m<sup>-2</sup>), number of taxa and Simpson's diversity index ( $1 - \lambda'$ ) (Simpson, 1949) were calculated to summarise different aspects of diversity. Simpson's index was chosen due to its robustness as a measure of diversity and ability to account for underlying abundance distributions (Magurran, 2004). These metrics were the mean values calculated for the five individual samples at each site.

Periphyton biomass, assessed as chlorophyll *a*, was used as a surrogate for primary productivity. Morin et al. (1999) reviewed the relationship between chlorophyll *a* and productivity in streams and found a strong link between the two ( $r^2 = 0.63$ ). Moreover, Tonkin (2011) found a strong link between biomass accumulation on artificial substrates and chlorophyll *a* on natural substrates ( $r^2 = 0.74$ ) in these streams. Periphyton biomass was estimated from measures of chlorophyll *a* from five stones (mean area: 60 cm<sup>2</sup>) collected randomly from each site. Stones were kept cool in the dark before being frozen. Chlorophyll *a* was extracted using 90% acetone at 5°C for 24 h in the dark. Absorbances were read on a Varian Cary 50 conc UV–Visible Spectrophotometer (Varian Australia Pty Ltd, Mulgrave, Australia) and converted to pigment concentration following Steinman and Lambert (1996). Stone surface area was estimated following Graham et al. (1988) and then halved to correct for the proportion of the stone available for periphyton growth.

### Physicochemical and substrate variables

Bed stability/substrate disturbance was assessed using the Pfankuch stability index (Pfankuch, 1975). Only the bottom component of the index (rock angularity, brightness, packing, percent stable materials, scouring

and amount of clinging vegetation) was used, as this is more relevant to stream invertebrate communities (Winterbourn & Collier, 1987; Death & Winterbourn, 1994).

Substrate size composition was assessed using the ‘Wolman Walk’ method where the beta axis of 100 stones was measured at approximately 1 m intervals across a zigzag transect at 45° to the stream bank (Wolman, 1954). Percentage substrate composition of Wentworth scale classes was converted to a single substrate size index by summing midpoint values of size classes weighted by their proportion. Bedrock was assigned a nominal size of 400 mm for use in the calculations.

Conductivity, temperature and pH were measured using Eutech instruments ECScan pocket meter. Depth and velocity were recorded with a Marsh-McBirney flowmate current meter in the thalweg of each stream at five equidistant intervals along the study reach. Flow type of each site was assessed visually as percentage of backwater, pool, run or riffle over a 100 m reach. Coarse particulate organic matter (CPOM) was assessed visually as the percent bed cover of leaf litter within the 50 m reach. Riparian vegetation percent composition (native forest, native scrub, planted forest, pasture and bare ground) and % canopy cover over the stream channel were also assessed visually.

In order to test for differences in the disturbance–productivity–diversity relationship between open canopy and sites with canopy cover, sites were split to create an open canopy and a canopy cover group differentiated at the median value of around 30% cover. Specifically, open canopy sites ( $n = 24$ ) were those with less than 30% overhead cover and sites with canopy cover ( $n = 23$ ) those with greater than or equal to 30% overhead cover. At 100% cover no overhead sky was visible, so 30% cover represented a significant amount of reduced light entering the stream. These groups were kept for all analyses, as well as carrying out analyses on the complete data set.

### Statistical analysis

To explore differences in community structure between open and closed canopy streams we carried out analysis of similarities (ANOSIM) (Clarke, 1993) on  $\log(x + 1)$  data using Bray–Curtis similarity in

Primer v6 (Clarke & Gorley, 2006). We then used similarity percentages (SIMPER) (Clarke, 1993) to explore which taxa contributed to the differences between canopy (Clarke & Gorley, 2006).

In order to test for differences in periphyton and diversity between open canopy and sites with canopy cover, we carried out analysis of variance (ANOVA) using Statistix (Statistix 8 ©, Analytical Software, Tallahassee, FL, USA). Differences in productivity between canopy types were determined with analysis of covariance (ANCOVA) with disturbance and stream width as covariates. If required, data were  $\log(x + 1)$  transformed to adjust for normality. Regressions and ANCOVA between disturbance, productivity and diversity were carried out in Statistix. Akaike’s Information Criterion (AIC) (Akaike, 1974), which accounts for goodness of fit and the number of model parameters, was used to determine the best fitting model.

When a significant quadratic term was present, we used the Mitchell-Olds and Shaw (MOS) test (Mitchell-Olds & Shaw, 1987) to test whether these quadratic relationships were true unimodal (hump-shaped) relationships or simply quadratic increases or declines. This test assesses whether ‘humps’ fall within the observed ranges of independent variables by testing whether the peak of the relationship and its confidence intervals are significantly higher than the minimum of the independent, and vice versa for the maximum. This analysis was carried out using the Vegan package (Oksanen et al., 2011) in R 2.13.1 (R Development Core Team, 2011). Quantile regression was performed on the 90th percentile ( $\tau = 0.9$ ) to test the upper limit of the relationship between bed stability and periphyton biomass using the Quantreg package (Koenker, 2011) in R (R Development Core Team, 2011).

The DEM predicts a unimodal relationship between diversity and productivity, disturbance and the interaction between productivity and disturbance. To test this we fitted our data to the following polynomial:

$$S = b_0 + b_1P + b_2C + b_3P^2 + b_4C^2 + b_4P \times C$$

where  $P$  is the disturbance assessed as the Pfankuch index bottom component and  $C$  is productivity assessed as chlorophyll  $a$  ( $\mu\text{g cm}^{-2}$ ). In order to explore the productivity–disturbance–diversity relationship further we developed the following models

based on regressions between the individual predictors and richness observed in the results:

Model 1

$$S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2 + b_4P \times C$$

Model 2

$$S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2$$

Model 1 has the interaction term between disturbance and productivity included and model 2 has the interaction excluded in order to explore the interactive c.f. additive effects of productivity and disturbance.

## Results

### Physicochemical conditions

Conductivity ranged from 40 to 298  $\mu\text{S cm}^{-1}$  and was higher in open than closed canopy streams (Table 1) but did not differ with the source of streams (i.e. runoff-fed, spring-fed, or dammed) ( $F_{2,44} = 0.92$ ,  $P = 0.41$ ). Spot temperature ranged from 6.6 to 17.6°C at all sites and was slightly lower in spring-fed streams ( $F_{2,44} = 3.29$ ,  $P = 0.047$ ) but did not differ with canopy cover (Table 1). Overhead cover did not differ with stream source ( $F_{2,44} = 1.12$ ,  $P = 0.33$ ). Mean velocity and depth ranged from 0.16 to 1.46  $\text{m s}^{-1}$  and 5.7 to 52.2 cm, respectively, and were greater in open canopy streams (Table 1). Overhead cover and stream width were negatively correlated ( $r = -0.45$ ,  $P = 0.001$ ), thus width was greater at open canopy sites (Table 1).

### Taxonomic composition

The presence or absence of canopy cover had a strong effect on community structure in these streams (ANOSIM  $R = 0.137$ ,  $P = 0.001$ ). Ephemeroptera, Plecoptera, Trichoptera and Chironomidae were the dominant taxa in all study sites. The mayfly *Deleatidium* spp., the stonefly *Zelandoperla* sp., the elmid beetle larvae *Hydora* spp. and the chironomid *Mao-ridiamesa* sp. displayed the greatest abundance at both open canopy and closed canopy sites (i.e. >3.7% relative abundance). No single taxon contributed more than 5% to the difference in community structure between open and closed canopy streams (SIMPER: avg. dissimilarity = 58.7). Four chironomid taxa were

amongst the top five contributors to differences in community structure between open and closed sites (>3.5% contribution to differences). The filter feeding mayfly *Coloburiscus humeralis* was strongly associated with sites with canopy cover (5.3% contribution) as were Oligochaeta (5.1% contribution), the mayfly *Austroclima sepia* (3.2% contribution) and the cased caddisfly *Beraeoptera roria* (3.6% contribution). The net-spinning caddisfly *Aoteapsyche colonica* (6.4% contribution) and the tipulid *Aphrophila neozelandica* (3.3% contribution) were found more commonly at open canopy sites.

### Periphyton and stability

Chlorophyll *a* ranged from 0.03 to 5.02  $\mu\text{g cm}^{-2}$  and averaged 1.87  $\mu\text{g cm}^{-2}$ . There was no difference in chlorophyll *a* (periphyton biomass) between open and closed sites (Table 1), with or without stream width as a covariate (ANCOVA:  $F_{1,44} = 0.33$ ,  $P = 0.57$ ). There was no linkage between chlorophyll *a* and the Pfankuch index with all sites included ( $r = -0.16$ ,  $P = 0.28$ ) or at closed canopy sites ( $r = 0.13$ ,  $P = 0.57$ ), but there was a negative correlation at open canopy sites ( $r = -0.41$ ,  $P = 0.046$ ). Sites with canopy cover were more stable (Pfankuch index; Table 1) but differences in site stability did not account for the differences in periphyton biomass between open canopy and closed canopy sites (ANCOVA:  $F_{1,44} = 0.14$ ,  $P = 0.71$ ). Periphyton biomass peaked at intermediate levels of stability (Pfankuch index) for all sites combined ( $F_{2,44} = 4.32$ ,  $P = 0.019$ ,  $r^2 = 0.16$ ,  $y = -1.57 + 0.25x - 0.004x^2$ ; Fig. 1). The upper regression quantile ( $\tau = 0.9$ ) clearly indicates a unimodal upper limit for the relationship between periphyton biomass and stability ( $y = -4.82 + 0.61x - 0.009x^2$ ). Periphyton biomass was not related to stability at closed canopy sites ( $F_{1,21} = 0.34$ ,  $P = 0.57$ ,  $r^2 = 0.02$ ; Fig. 1), but was lower at open sites with decreased stability ( $F_{1,22} = 4.46$ ,  $P = 0.05$ ,  $r^2 = 0.17$ ,  $y = 4.04 - 0.06x$ ; Fig. 1). CPOM was not related to stability for all sites ( $F_{1,45} = 0.46$ ,  $P = 0.5$ ), and for open ( $F_{1,22} = 0.62$ ,  $P = 0.44$ ) or closed ( $F_{1,21} = 2.73$ ,  $P = 0.11$ ) canopy sites.

### Density and diversity

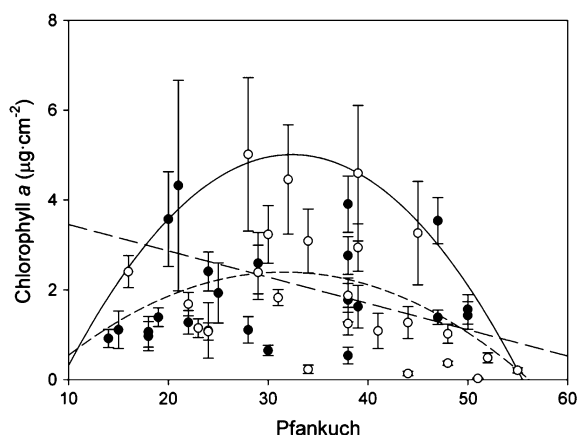
The mean total density of invertebrates in the benthos ranged from 3.8 to 1,205 individuals  $0.1 \text{ m}^{-2}$  and did

**Table 1** Mean ( $\pm 1$  SE) physicochemical, periphyton and invertebrate community characteristics for open and closed canopy streams collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007

*F* and *P* values for one-way ANOVA testing for differences between open and canopy streams are also given

*SI* substrate size index, *CPOM* coarse particulate organic matter

	Open canopy	Closed canopy	$F_{1,45}$	<i>P</i>
Width (m)	12.9 (1.95)	5.63 (1.03)	10.63	0.002
Depth (cm)	31.05 (1.85)	23.16 (2.42)	6.77	0.013
Velocity ( $\text{m s}^{-1}$ )	0.89 (0.04)	0.67 (0.08)	6.53	0.014
Conductivity ( $\mu\text{S cm}^{-1}$ )	131.58 (14.15)	93.17 (7.66)	5.56	0.023
Temperature ( $^{\circ}\text{C}$ )	10.71 (0.45)	10.87 (0.44)	0.06	0.8
pH	7.88 (0.12)	8.03 (0.06)	1.14	0.29
Substrate size index	152.59 (9.02)	134.98 (11.21)	1.51	0.23
CPOM (%)	2.46 (0.99)	12.48 (2.93)	10.88	0.002
Slope (m/10 m)	3.77 (0.35)	4.87 (0.5)	3.34	0.074
Pfankuch score	36.88 (2.12)	30.09 (2.42)	4.48	0.04
Chlorophyll <i>a</i> ( $\mu\text{g cm}^{-2}$ )	1.88 (0.3)	1.87 (0.23)	<0.01	0.98
No. of taxa $0.1 \text{ m}^{-2}$	14.78 (1.02)	18.02 (0.91)	5.6	0.022
No. of individuals $0.1 \text{ m}^{-2}$	327.5 (59.52)	275.92 (32.15)	0.57	0.46
Simpson's ( $1 - \lambda'$ )	0.74 (0.02)	0.81 (0.01)	9.52	0.004



**Fig. 1** Mean ( $\pm 1$  SE) chlorophyll *a* as a function of the bottom component of the Pfankuch stability index collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007. *Open circles* are open canopy streams and *closed circles* are sites with canopy cover. *Solid line* is the 90th regression quantile, *short dashed line* is the least squares regression for the mean of all sites, *long dashed line* is the regression for open canopy sites only; see text for least squares statistics. Quantile regression coefficients ( $\pm 1$  SE): Intercept =  $-4.82$  (2.34),  $t = -2.06$ ,  $P = 0.046$ , 95% CI =  $-5.27$ – $19.39$ ; Pfankuch =  $0.61$  (0.15),  $t = 3.96$ ,  $P = 0.0003$ , 95% CI =  $-0.04$ – $0.65$ ; Pfankuch<sup>2</sup> =  $-0.009$  (0.002),  $t = -4.12$ ,  $P = 0.0002$ , 95% CI =  $-0.01$ – $0.00303$

not differ between open and closed canopy sites (Table 1). Density increased logarithmically with increasing periphyton biomass and declined at an increasing rate with increasing disturbance levels (Table 2). If open canopy sites were considered

separately, density also increased logarithmically with increasing periphyton biomass (Fig. 2; Table 2) and peaked at low to intermediate levels of stability (Fig. 2; Table 2; AIC:  $-33.3$ ) rather than declining monotonically ( $F_{1,22} = 12.92$ ,  $P = 0.001$ ,  $r^2 = 0.37$ ; AIC:  $-32.4$ ). A MOS test confirmed this relationship was not unimodal but a quadratic decline ( $P = 0.33$ ). No relationship with periphyton biomass or stability was evident at closed canopy sites (Fig. 2; Table 2). The number of individuals was not related to CPOM at all sites ( $F_{1,45} = 0.04$ ,  $P = 0.84$ ), and at open ( $F_{1,22} = 0.01$ ,  $P = 0.94$ ) or closed ( $F_{1,21} = 0.03$ ,  $P = 0.87$ ) canopy sites.

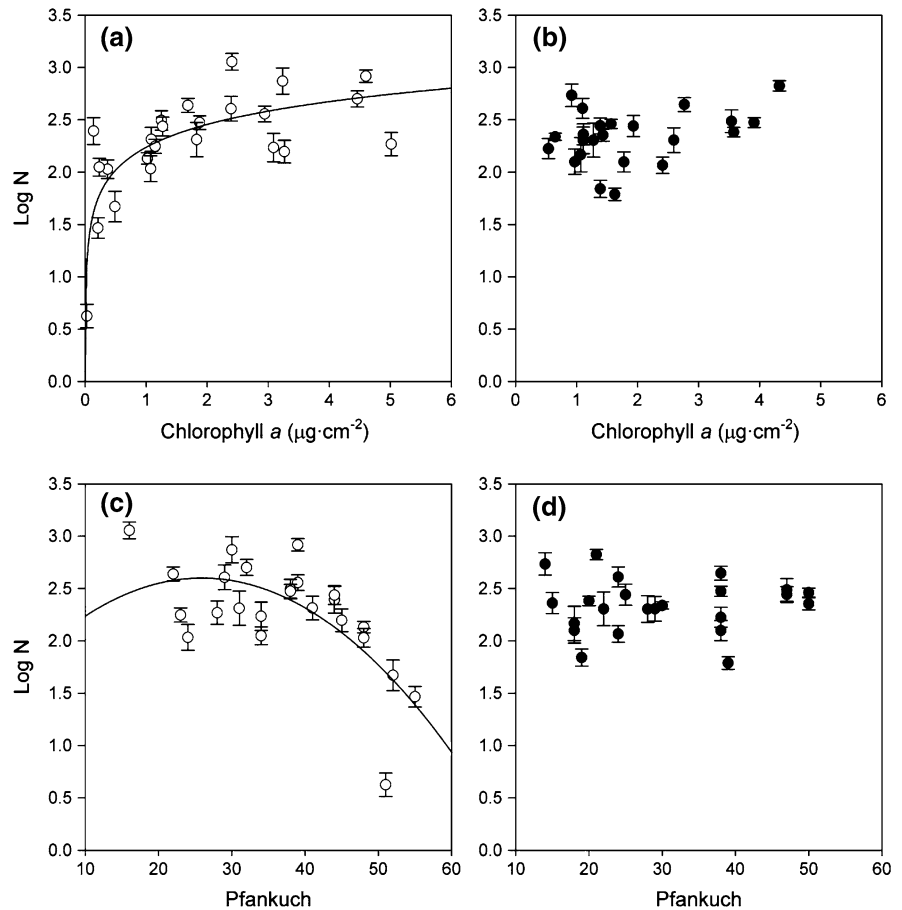
The mean number of taxa collected per sample averaged  $16.4$  taxa  $0.1 \text{ m}^{-2}$  ranging from  $2.2$  to  $27.8$  taxa  $0.1 \text{ m}^{-2}$ . Taxonomic richness was higher at closed than open canopy sites (Table 1). Richness increased logarithmically with increasing periphyton biomass and peaked at intermediate levels of disturbance (Table 2). A MOS test confirmed this relationship was unimodal, peaking within the observed range of disturbance measures ( $P = 0.003$ ). With open canopy sites considered separately, richness increased logarithmically with increasing periphyton biomass and peaked at intermediate levels of disturbance (Fig. 3; Table 2). No relationship with periphyton biomass or stability was found at closed canopy sites (Fig. 3; Table 2). Taxonomic richness was not related to CPOM at all sites ( $F_{1,45} = 3.79$ ,  $P = 0.058$ ), and at open ( $F_{1,22} = 1.47$ ,  $P = 0.24$ ) or closed ( $F_{1,21} = 0.49$ ,  $P = 0.49$ ) canopy sites.

**Table 2** Results of regression analysis for mean number of individuals (density) and mean number of taxa as a function of (a) bottom component of the Pfanckuch stability index and (b) chlorophyll *a* ( $\mu\text{g cm}^{-2}$ ) collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007

	df	F	P	r <sup>2</sup>	Equation
<b>(a) Pfanckuch</b>					
Density	2, 44	6.21	0.004	0.23	$y = 1.74 + 0.054x - 0.001x^2$
Open canopy	2, 21	9.43	0.001	0.47	$y = 1.64 + 0.07x - 0.001x^2$
Closed canopy	1, 21	0.01	0.91	0.0006	Non-significant
No. of taxa	2, 44	7.01	0.002	0.24	$y = 9.90 + 0.64x - 0.01x^2$
Open canopy	2, 21	13.42	0.0002	0.56	$y = -10.59 + 1.76x - 0.03x^2$
Closed canopy	1, 21	1.20	0.29	0.05	Non-significant
<b>(b) Chlorophyll <i>a</i></b>					
Density	1, 45	42.23	<0.0001	0.48	$y = 2.22 + 0.28\ln(x)$
Open canopy	1, 22	36.07	<0.0001	0.62	$y = 2.24 + 0.31\ln(x)$
Closed canopy	1, 21	2.99	0.099	0.13	Non-significant
No. of taxa	1, 45	25.54	<0.0001	0.36	$y = 15.48 + 2.97\ln(x)$
Open canopy	1, 22	22.93	<0.0001	0.51	$y = 14.41 + 2.79\ln(x)$
Closed canopy	1, 21	4.22	0.053	0.17	Non-significant

df degrees of freedom

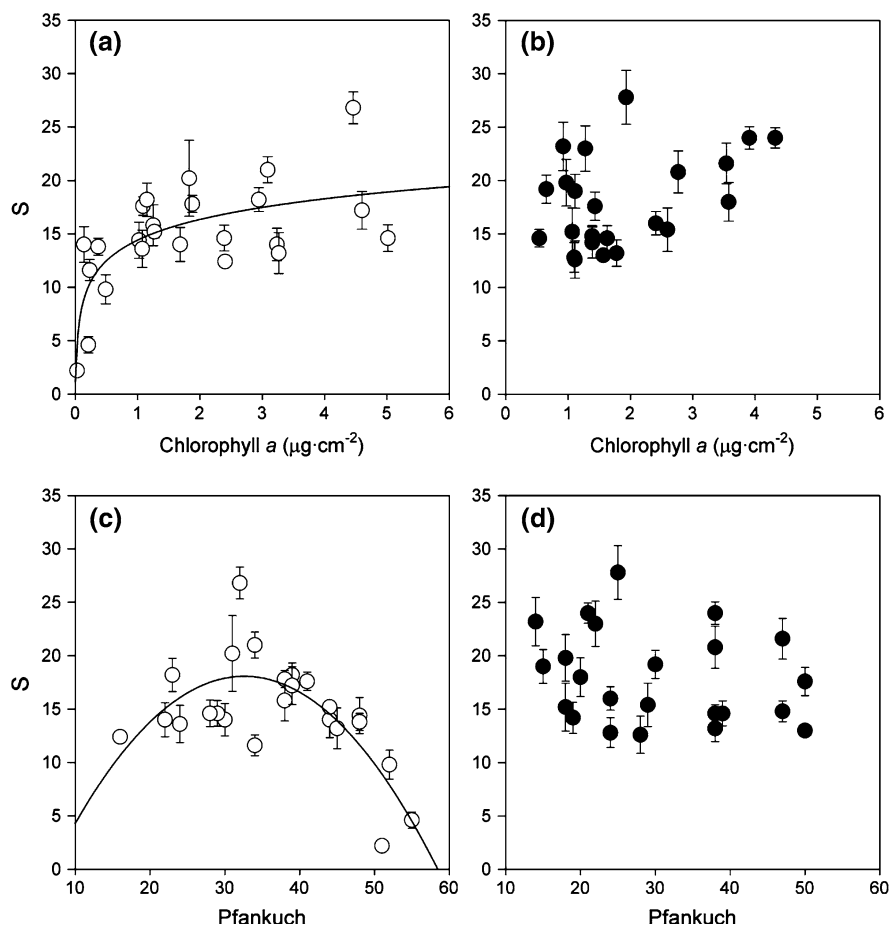
**Fig. 2** Mean ( $\pm 1$  SE) log number of animals as a function of **a, b** chlorophyll *a* and **c, d** bottom component of Pfanckuch stability index collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007. **a, c** Open canopy sites and **b, d** sites with canopy cover. See Table 2 for regression results



Simpson's diversity index was higher at sites with canopy cover than open canopy sites (Table 1), and declined with decreasing stability when all sites were

considered together ( $F_{1,45} = 6.94$ ,  $P = 0.01$ ,  $r^2 = 0.13$ ;  $y = 0.866 - 0.00263x$ ). This declining trend in Simpson's index with stability was significant at

**Fig. 3** Mean ( $\pm 1$  SE) number of taxa as a function of (a, b) chlorophyll *a* and c, d bottom component of Pfankuch stability index collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007. a, c Open canopy sites and b, d sites with canopy cover. See Table 2 for regression results



closed ( $F_{1,45} = 13.15$ ,  $P = 0.002$ ,  $r^2 = 0.39$ ;  $y = 0.9 - 0.00291x$ ) but not at open ( $F_{1,45} = 0.14$ ,  $P = 0.71$ ,  $r^2 = 0.006$ ) canopy sites. Simpson's index was not related to periphyton biomass at all sites ( $F_{1,45} = 0.05$ ,  $P = 0.83$ ,  $r^2 = 0.001$ ), and at open ( $F_{1,45} = 0.0006$ ,  $P = 0.98$ ,  $r^2 = 0.00003$ ) or closed ( $F_{1,45} = 0.28$ ,  $P = 0.6$ ,  $r^2 = 0.013$ ) canopy sites. Similarly, Simpson's index was not related to CPOM at all sites ( $F_{1,45} = 0.08$ ,  $P = 0.78$ ), and at open ( $F_{1,22} = 0.03$ ,  $P = 0.86$ ) or closed ( $F_{1,21} = 2.88$ ,  $P = 0.1$ ) canopy sites.

#### Model testing

With all sites included, AIC identified Model 2 ( $P \times D$  interaction excluded) as the best model (AIC = 63.5), followed by Model 1 ( $P \times D$  interaction included) (AIC = 65.4) and then the DEM (AIC = 67.6). At only open canopy sites, Model 2

was again the most parsimonious (AIC = -16.4), followed by Model 1 (AIC = 32.4) and then the DEM (AIC = 36.7).

Fitting all sites to the DEM ( $S = b_0 + b_1P + b_2C + b_3P^2 + b_4C^2 + b_5P \times C$ ) explained 42% of the variation in the data ( $F_{5,41} = 5.84$ ,  $P = 0.0004$ ,  $r^2 = 0.42$ ; Fig. 4; Table 3), however, the only significant coefficient was the intercept (Table 3). For only open canopy sites, the DEM explained 63% of the variation in richness ( $F_{5,18} = 6.07$ ,  $P = 0.002$ ,  $r^2 = 0.63$ ; Fig. 4; Table 3) with only the Pfankuch and Pfankuch<sup>2</sup> coefficients significant. The DEM did not fit the data at sites with canopy cover ( $F_{5,17} = 1.88$ ,  $P = 0.15$ ,  $r^2 = 0.36$ ).

Model 1, with the interaction between productivity and disturbance included ( $S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2 + b_4P \times C$ ), explained 70% of the variation in the open canopy data ( $F_{4,19} = 11.21$ ,  $P < 0.0001$ ,  $r^2 = 0.70$ ; Fig. 4; Table 3) and the same amount of variation



(42%) as in the DEM for all sites ( $F_{4,42} = 7.6$ ,  $P = 0.0001$ ,  $r^2 = 0.42$ ; Fig. 4; Table 3). However, the interaction between productivity and disturbance in both the open canopy sites and the all sites data set was not significant. There was no fit at closed canopy sites ( $F_{5,17} = 2.41$ ,  $P = 0.09$ ,  $r^2 = 0.35$ ).

Model 2 with the interaction between productivity and disturbance excluded ( $S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2$ ) decreased the overall fit slightly to 68% of the variation in richness at open canopy sites but the three coefficients other than intercept were significant ( $F_{3,20} = 14.36$ ,  $P < 0.0001$ ,  $r^2 = 0.68$ ; Fig. 4; Table 3). The fit once more stayed the same as the previous two models with all data included ( $F_{3,43} = 10.26$ ,  $P < 0.0001$ ,  $r^2 = 0.42$ ; Fig. 4; Table 3), and did not fit closed canopy sites ( $F_{5,17} = 1.69$ ,  $P = 0.2$ ,  $r^2 = 0.21$ ).

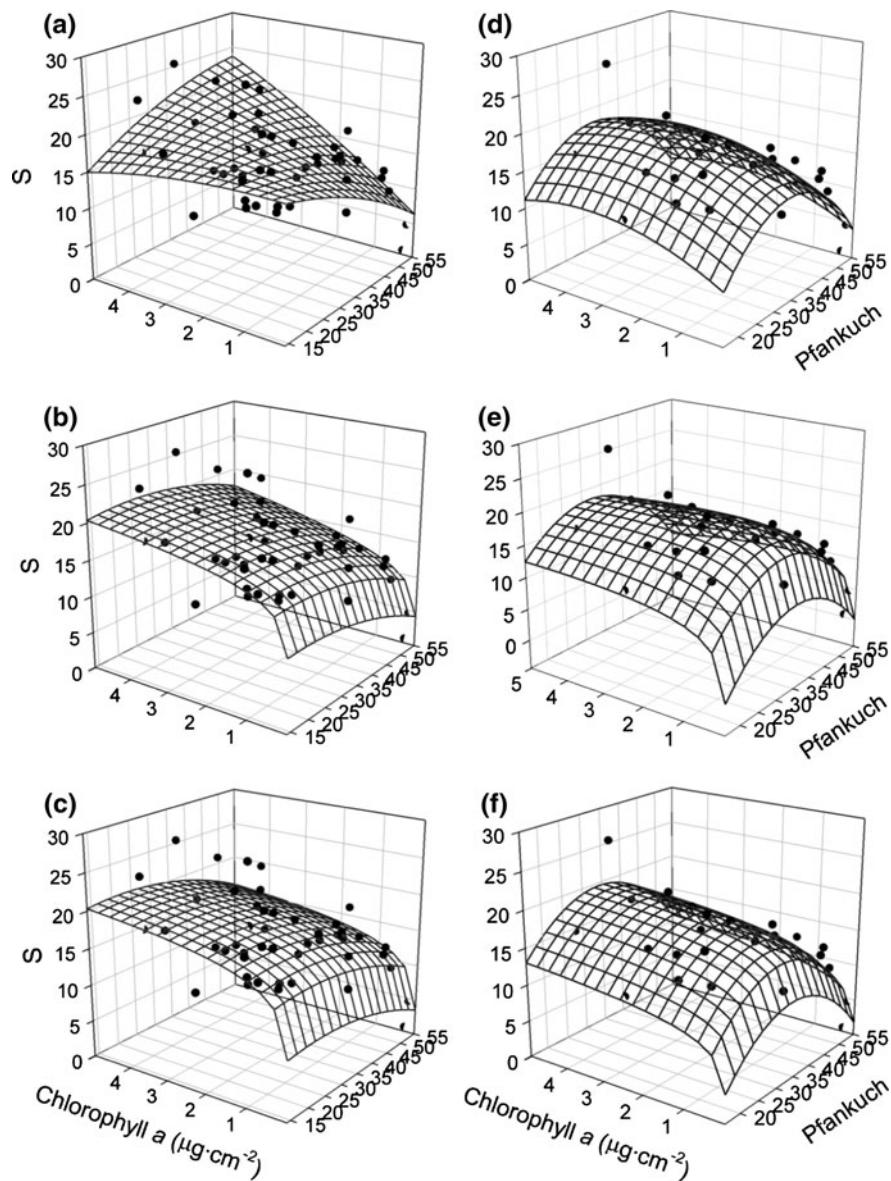
## Discussion

The relationship between richness, stability and productivity in these mountain streams was dictated by overhead cover. The fit to the DEM was better at open canopy sites than sites with canopy cover, and richness was related to productivity and stability only at open canopy sites. In contrast to the patterns observed with taxonomic richness, Simpson's diversity index declined with decreasing stability only for streams with canopy cover. Although overhead cover was related to stream size, providing stream size as a covariate did not alter the relationship between periphyton biomass and canopy cover. Previous studies have found that canopy cover can alter the effects of floods on stream invertebrate communities (likely through the limitation of available light) (Robinson & Minshall, 1986; Death, 2002; Death & Zimmermann, 2005; Fuller et al., 2008). Most of these studies found that floods reduce periphyton and invertebrate diversity at open canopy sites, while at sites with canopy cover, periphyton and invertebrate communities showed little or no change (Death, 2002; Death & Zimmermann, 2005; Fuller et al., 2008). In the absence of forest canopy, periphyton is the dominant food source for invertebrates in stony streams whereas under canopy it is only one of several potential food sources. Thus invertebrates would be expected to be more tightly linked with algal productivity gradients in open canopy streams, than in those

with canopy cover. The high mobility of lotic invertebrates allows for rapid recolonisation after disturbance but is dependent, amongst other things, on resource recovery (e.g. periphyton) (Mackay, 1992; Allan, 1995; Death & Zimmermann, 2005). As such, in streams with canopy cover where periphyton resources are low, the rate of recovery will be independent of algal productivity. The streams in this study are likely to be nutrient limited as they are pristine mountain streams and so we would expect periphyton recovery to be slower than in nutrient enriched streams after any disturbance.

Although the density of overhead canopy in many New Zealand forests means periphyton standing crops are often low (Winterbourn, 1990; Death & Zimmermann, 2005), there was no effect of canopy cover on algal productivity in the streams we studied. This may be the result of nutrient limitation in open streams or recent disturbance events removing periphyton, although this was not evident at sampling (JDT, pers. obs.). Alternatively, it could be a result of differences in algal quality between open and closed canopy streams such as that found with communities dominated by grazing resistant basal cells of the filamentous green alga *Stigeoclonium* in the absence of light (Steinman et al., 1990; Barquin, 2004). Nonetheless, productivity declined with disturbance at open but not closed canopy sites, which may be due, in part, to the fact that the sites with canopy cover were more stable.

Streams with canopy cover may comprise communities more resistant to pulsed disturbances than open canopy streams as long as organic matter is retained during floods or that as much organic matter is washed in as is washed out (Fuller et al., 2008). We found no relationship between stability and CPOM, or between CPOM and invertebrate community diversity. We did not measure FPOM, which is generally unaffected by disturbance in New Zealand streams (Scrimgeour & Winterbourn, 1989; Death & Winterbourn, 1995), and several studies have found that POM is not related to the stability of both open and closed canopy New Zealand streams (Scrimgeour & Winterbourn, 1989; Death & Zimmermann, 2005). This absence of linkage between CPOM and invertebrate community diversity may be a result of the comparatively low level of allochthonous material entering or being retained in New Zealand streams which in turn results in less obligate shredders (Winterbourn et al., 1981; Winterbourn, 1997).



**Fig. 4** Taxonomic richness as a function of chlorophyll *a* and the bottom component of the Pfankuch stability index for **a–c** all sites and **d–f** open canopy sites only collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007. **a, d** DEM ( $S = b_0 + b_1P + b_2C + b_3P^2 + b_4C^2 + b_5P \times C$ ); **b, e** model 1—with productivity  $\times$

disturbance interaction ( $S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2 + b_4P \times C$ ) and **c, f** model 2—without productivity  $\times$  disturbance interaction ( $S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2$ ) where  $P =$  Pfankuch and  $C =$  chlorophyll *a*. See Table 3 for coefficients and text for model fit

#### Specific effects of disturbance and productivity

Diversity peaked at intermediate levels of disturbance as predicted by the IDH and DEM. The most widely accepted view of how disturbance affects diversity is that it creates new niche opportunities by removing

taxa and interrupting biological processes such as competitive exclusion (Connell, 1978; Huston, 1979, 1994; Cadotte, 2007). These opportunities allow for the greatest expression of life history traits at intermediate levels of disturbance. Conversely, in systems where competitive exclusion is less prevalent

**Table 3** Coefficients for the three models of taxonomic richness as a function of chlorophyll *a* and the bottom component of the Pfankuch stability index on invertebrate communities collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007. (a) DEM ( $S = b_0 + b_1P + b_2C + b_3P^2 + b_4C^2 +$

$b_5P \times C$ ), (b) model 1—with productivity  $\times$  disturbance interaction ( $S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2 + b_4P \times C$ ) and (c) model 2—without productivity  $\times$  disturbance interaction ( $S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2$ ) where  $P =$  Pfankuch and  $C =$  chlorophyll *a* ( $\mu\text{g cm}^{-2}$ )

Model	All sites			Open canopy		
	Coefficient (SE)	<i>t</i>	<i>P</i>	Coefficient (SE)	<i>t</i>	<i>P</i>
(a) DEM						
$b_0$	19.09 (6.99)	2.73	<0.01	-11.35 (14.06)	-0.81	0.43
$b_1$	-0.03 (0.39)	-0.09	0.93	1.50 (0.67)	2.24	0.04
$b_2$	-1.20 (3.01)	-0.40	0.69	3.14 (4.69)	0.67	0.51
$b_3$	-0.004 (0.005)	-0.67	0.51	-0.02 (0.008)	-2.70	0.01
$b_4$	-0.15 (0.38)	-0.40	0.69	-0.45 (0.43)	-1.05	0.31
$b_5$	0.10 (0.05)	1.87	0.07	-0.002 (0.09)	-0.02	0.98
(b) Model 1 (interaction)						
$b_0$	15.19 (5.53)	2.75	<0.01	-9.03 (7.50)	-1.20	0.24
$b_1$	0.15 (0.37)	0.40	0.69	1.55 (0.46)	3.38	<0.01
$b_2$	1.88 (1.28)	1.47	0.15	2.80 (1.11)	2.52	0.02
$b_3$	-0.004 (0.005)	-0.76	0.45	-0.02 (0.006)	-3.48	<0.01
$b_4$	0.01 (0.03)	0.46	0.65	-0.02 (0.02)	-1.11	0.28
(c) Model 2 (no interaction)						
$b_0$	14.6 (5.32)	2.74	<0.01	-6.56 (7.22)	-0.91	0.37
$b_1$	0.20 (0.35)	0.57	0.58	1.36 (0.43)	3.18	<0.01
$b_2$	2.38 (0.66)	3.40	<0.001	1.79 (0.65)	2.77	0.01
$b_3$	-0.004 (0.005)	-0.85	0.4	-0.02 (0.006)	-3.28	<0.01

or absent, disturbance may simply be resetting the colonisation process by removing animals and their resource supply (Death, 2002). This mechanism has been shown to occur in streams with productivity setting the upper limit to richness rather than leading to competitive exclusion (Death, 2002). Although evidence from our study suggests that disturbance is acting along the lines predicted by the DEM and IDH, no taxa demonstrated strong trends for either end of the disturbance continuum. Rather, what appears to be evident is a large proportion of taxa are common at moderately disturbed sites but less so at either stable or unstable sites. The few taxa to demonstrate any relationship were the midges *Maoridiamesa* sp. and one species of Orthocladiinae, and the helicophid caddisfly *Zelolessica cheira* which declined with disturbance whereas the tipulid Eriopterini increased. Moreover, the taxa exhibiting trends for either end of the disturbance continuum appear to be influenced by specific habitat preferences rather than a competitive hierarchy. For example, *Z. cheira* favours bryophytes

which are associated with stable spring-fed streams and *Maoridiamesa* is often associated with cold stable temperature regimes of spring-fed streams (Barquin & Death, 2006).

The DEM predicts diversity will exhibit a unimodal relationship with productivity, depending on the level of disturbance and vice versa. However, in the present study, richness and density both increased logarithmically with increasing rates of productivity, while evenness (Simpson's index) was not related to productivity. This logarithmic increase in diversity suggests, rather than productivity controlling the rate of displacement of inferior competitors by superior competitors as predicted by the DEM, productivity is setting the upper limit to the potential richness of a community, as proposed by Death (2002). One possible explanation for the non-uniform responses may be the scale at which a system is observed (Chase & Leibold, 2002). Additionally, as with disturbance, if the community comprises highly mobile taxa in an open environment such as streams, it is likely that

competitive exclusion will not be invoked at higher productivity and thus unimodal relationships will be unlikely. Lack of trophic specialisation in New Zealand stream invertebrates generally, and the dependence on a trade-off between traits such as competitive and colonising abilities (Chesson & Huntly, 1997; Roxburgh et al., 2004; Cadotte, 2007), suggests leading diversity models may be unsuitable for these communities.

### Interactions between productivity and disturbance

Both the DEM and our model incorporating a log-linear productivity–diversity relationship displayed no interaction between productivity and stability. This lack of interaction was surprising firstly because these factors should theoretically be complementary, with disturbances creating niches and productivity controlling the rate of colonisation; and secondly because the main effect of disturbance in streams is through the removal of the food supply (periphyton) rather than the direct removal of animals (Death, 2002). Using protozoan communities in the laboratory, Scholes et al. (2005) concluded similarly that diversity responded to both productivity and disturbance without any interacting effects. The DEM predicts that both the productivity–richness and disturbance–richness relationships are unimodal, and that the level of one factor interacts with the other to influence where the peak of that relationship forms. Thus, productivity and disturbance theoretically interact to allow for the greatest variety of life history traits to be expressed. Perhaps, because of an absence of a competition–colonisation trade-off in these streams, this interaction cannot occur and the greatest diversity is simply at high productivities where resources are allowing more animals to coexist.

It is important to note here that a robust test of the DEM, and any multiple regression in fact, requires dependent variables to be orthogonal (Quinn & Keogh, 2002). The relationship between productivity and disturbance in this study was weak and only evident at open canopy sites. Yet, a clearly unimodal upper-limit relationship was observed for all sites. Assessing the DEM in widespread surveys of this nature is complicated by the requirement of covering all four corners of the productivity–disturbance spectrum. In this study there were few sites at the high-productivity high-disturbance corner of the spectrum

suggesting results found here may be more specific to low productivity/stochastic systems such as alpine streams (Milner & Petts, 1994; Gafner & Robinson, 2007). Consequently, the logarithmic increase in richness with productivity that we found may represent the peak in a greater unimodal relationship and an interaction between productivity and disturbance may well have occurred across a broader range of conditions. Nevertheless, for the streams included in this study, our model suggests that, rather than shifting the peak in diversity, productivity increases logarithmically the magnitude of a unimodal disturbance–diversity curve. Essentially macroinvertebrate community richness peaked at intermediate levels of disturbance with productivity determining the magnitude of that peak.

### Conclusions

In summary, we found little evidence to support the DEM within the range of conditions encountered and other models were more appropriate for the systems. Although collinearity between productivity and disturbance and the limited range of productivity encountered potentially hampered the assessment of the DEM within these systems, productivity and disturbance were shown to be important determinants of richness. We suggest that productivity and disturbance act independently of each other and are not sufficient to explain patterns in these mountain streams in isolation of other factors. Accordingly, it appears more complex multivariate models than those such as the DEM are required to adequately explain diversity in these natural systems. Our model suggests richness peaks at intermediate levels disturbance in autotrophic streams with productivity determining the peak of the curve, but no statistical evidence of an interaction with disturbance regulating diversity patterns.

**Acknowledgments** We are grateful to Keith Wood at Ernslaw One Limited for access to Karioi Forest sites. We are also grateful to Roger Tonkin, Amber McEwan, Nicki Atkinson, Manas Chakraborty, Robert Charles, Logan Brown, and Alana Lawrence for assistance in the field. Michel Dedual, Glenn Mclean and Mike Joy provided logistical support during the site selection and fieldwork stages. Thanks to Jane Tonkin for reviewing a draft copy of this manuscript. Angus McIntosh, Ian Henderson and Christopher Robinson provided useful

comments to improve this manuscript. Massey University Doctoral Scholarship supported JDT during the study.

## References

- Abrams, P. A., 1995. Monotonic or unimodal diversity productivity gradients—What does competition theory predict. *Ecology* 76: 2019–2027.
- Akaike, H., 1974. New look at statistical-model identification. *IEEE Transactions on Automatic Control* AC19: 716–723.
- Allan, J. D., 1995. *Stream Ecology: Structure and Function of Running Waters*. Chapman and Hall, London.
- Barquin, J., 2004. Spatial patterns of invertebrate communities in spring and runoff-fed streams. PhD thesis, Massey University, New Zealand.
- Barquin, J. & R. G. Death, 2006. Spatial patterns of macroinvertebrate diversity in New Zealand springbrooks and rhithral streams. *Journal of the North American Benthological Society* 25: 768–786.
- Cadotte, M. W., 2007. Competition-colonization trade-offs and disturbance effects at multiple scales. *Ecology* 88: 823–829.
- Cardinale, B. J., H. Hillebrand & D. F. Charles, 2006. Geographic patterns of diversity in streams are predicted by a multivariate model of disturbance and productivity. *Journal of Ecology* 94: 609–618.
- Chase, J. M. & M. A. Leibold, 2002. Spatial scale dictates the productivity–biodiversity relationship. *Nature* 416: 427–430.
- Chesson, P. & N. Huntly, 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist* 150: 519–553.
- Clarke, K. R., 1993. Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Clarke, K. R. & R. N. Gorley, 2006. *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth.
- Connell, J. H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.
- Currie, D. J., 1991. Energy and large-scale patterns of animal-species and plant-species richness. *American Naturalist* 137: 27–49.
- Death, R. G., 2002. Predicting invertebrate diversity from disturbance regimes in forest streams. *Oikos* 97: 18–30.
- Death, R. G., 2010. Disturbance and riverine benthic communities: what has it contributed to general ecological theory? *River Research and Applications* 26: 15–25.
- Death, R. G. & M. J. Winterbourn, 1994. Environmental stability and community persistence: a multivariate perspective. *Journal of the North American Benthological Society* 13: 125–139.
- Death, R. G. & M. J. Winterbourn, 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* 76: 1446–1460.
- Death, R. G. & E. M. Zimmermann, 2005. Interaction between disturbance and primary productivity in determining stream invertebrate diversity. *Oikos* 111: 392–402.
- Fuller, R. L., C. LaFave, M. Anastasi, J. Molina, H. Salcedo & S. Ward, 2008. The role of canopy cover on the recovery of periphyton and macroinvertebrate communities after a month-long flood. *Hydrobiologia* 598: 47–57.
- Gafner, K. & C. T. Robinson, 2007. Nutrient enrichment influences the responses of stream macroinvertebrates to disturbance. *Journal of the North American Benthological Society* 26: 92–102.
- Graham, A. A., D. J. McCaughan & F. S. McKee, 1988. Measurement of surface area of stones. *Hydrobiologia* 157: 85–87.
- Grime, J. P., 1973. Control of species density in herbaceous vegetation. *Journal of Environmental Management* 1: 151–167.
- Haddad, N. M., M. Holyoak, T. M. Mata, K. F. Davies, B. A. Melbourne & K. Preston, 2008. Species' traits predict the effects of disturbance and productivity on diversity. *Ecology Letters* 11: 348–356.
- Hastings, A., 1980. Disturbance, coexistence, history, and competition for space. *Theoretical Population Biology* 18: 363–373.
- Hubbell, S. P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Huston, M., 1979. A general hypothesis of species diversity. *The American Naturalist* 113: 81–100.
- Huston, M., 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.
- Koenker, R., 2011. *quantreg: Quantile Regression*. R package version 4.71.
- Kondoh, M., 2001. Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268: 269–271.
- Lake, P. S., 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19: 573–592.
- Mackay, R. J., 1992. Colonization by lotic macroinvertebrates—a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 617–628.
- Mackey, R. L. & D. J. Currie, 2001. The diversity–disturbance relationship: is it generally strong and peaked? *Ecology* 82: 3479–3492.
- Magurran, A. E., 2004. *Measuring Biological Diversity*. Blackwell Science Ltd., Oxford.
- Milner, A. M. & G. E. Petts, 1994. Glacial rivers—physical habitat and ecology. *Freshwater Biology* 32: 295–307.
- Mitchell-Olds, T. & R. G. Shaw, 1987. Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution* 41: 1149–1161.
- Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson & L. Gough, 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.
- Morin, A., W. Lamoureaux & J. Busnarda, 1999. Empirical models predicting primary productivity from chlorophyll a and water temperature for stream periphyton and lake and ocean phytoplankton. *Journal of the North American Benthological Society* 18: 299–307.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry,

- H. Stevens & H. Wagner, 2011. *Vegan: Community Ecology Package*. R package version 2.0-1.
- Pfankuch, D., 1975. Stream Reach Inventory and Channel Stability Evaluation. USDA Forest Service Region 1, Missoula, Montana.
- Quinn, G. P. & M. Keogh, 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- R Development Core Team, 2011. *R: A Language and Environment for Statistical Computing*. R Foundation of Statistical Computing, Vienna, Austria.
- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace & R. C. Wissmar, 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7: 433–455.
- Robinson, C. T. & G. W. Minshall, 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. *Journal of the North American Benthological Society* 5: 237–248.
- Rosenzweig, M. L., 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Rosenzweig, M. L. & Z. Abramsky, 1993. How are diversity and productivity related? In Ricklefs, R. E. & D. Schluter (eds), *Species Diversity in Biological Communities*. University of Chicago Press, Chicago, IL: 52–65.
- Roxburgh, S. H., K. Shea & J. B. Wilson, 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85: 359–371.
- Scholes, L., P. H. Warren & A. P. Beckerman, 2005. The combined effects of energy and disturbance on species richness in protist microcosms. *Ecology Letters* 8: 730–738.
- Scrimgeour, G. J. & M. J. Winterbourn, 1989. Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia* 171: 33–44.
- Simpson, E. H., 1949. Measurement of diversity. *Nature* 163: 688.
- Sousa, W. P., 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60: 1225–1239.
- Steinman, A. D. & G. A. Lamberti, 1996. Biomass and pigments of benthic algae. In Hauer, F. R. & G. A. Lamberti (eds), *Methods in Stream Ecology*. Academic Press, San Diego, CA: 295–314.
- Steinman, A. D., P. J. Mulholland, A. V. Palumbo, T. F. Flum, J. W. Elwood & D. L. Deangelis, 1990. Resistance of lotic ecosystems to a light elimination disturbance—a laboratory stream study. *Oikos* 58: 80–90.
- Svensson, J. R., M. Lindegarth, M. Siccha, M. Lenz, M. Molis, M. Wahl & H. Pavia, 2007. Maximum species richness at intermediate frequencies of disturbance: Consistency among levels of productivity. *Ecology* 88: 830–838.
- Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2–16.
- Tonkin, J. D., 2011. The effects of productivity and disturbance on diversity in stream communities. PhD thesis, Massey University, New Zealand.
- Towns, D. R. & W. L. Peters, 1996. *Leptophlebiidae (Insecta: Ephemeroptera)*, Vol. 36. Manaaki Whenua Press, Lincoln, New Zealand.
- Townsend, C. R., M. R. Scarsbrook & S. Doledec, 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* 42: 938–949.
- Winterbourn, M. J., 1990. Interactions among nutrients, algae and invertebrates in a New Zealand mountain stream. *Freshwater Biology* 23: 463–474.
- Winterbourn, M. J., 1997. New Zealand mountain stream communities: stable yet disturbed? In Streit, B., T. Stadler & C. M. Lively (eds), *Evolutionary Ecology of Freshwater Animals*. Birkhauser Verlag, Basel: 31–54.
- Winterbourn, M. J. & K. J. Collier, 1987. Distribution of benthic invertebrates in acid, brown water streams in the South Island of New Zealand. *Hydrobiologia* 153: 277–286.
- Winterbourn, M. J., J. S. Rounick & B. Cowie, 1981. Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* 15: 321–328.
- Winterbourn, M. J., K. L. D. Gregson & C. H. Dolphin, 2000. *Guide to the aquatic insects of New Zealand*. Entomological Society of New Zealand, Auckland.
- Wolman, M. J., 1954. A method of sampling coarse river bed material. *Transactions of the American Geophysical Union* 35: 951–956.
- Wootton, J. T., 1998. Effects of disturbance on species diversity: a multitrophic perspective. *American Naturalist* 152: 803–825.