

## Consistent effects of productivity and disturbance on diversity between landscapes

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**Abstract.** Productivity and disturbance have a strong role in determining diversity patterns in nature yet whether they operate individually or interact to determine diversity is unclear. Moreover, what effect land-use change has on this relationship has not been assessed. We tested whether land use influenced the relationship between productivity, disturbance and diversity, and assessed the fit of three productivity-disturbance-diversity models, using data from multiple samplings of 16 streams in two contrasting regions of the North Island of New Zealand. As the Dynamic Equilibrium Model (DEM) has received inconsistent support in all ecosystems and little favorable applications in lotic systems, we applied this along with two previously developed for stream communities. Although the community structure differed between the two regions, the response of taxonomic richness to productivity and disturbance was consistent. That is, richness was log-linearly related to productivity and declined monotonically with disturbance. However, there was no evidence of an interactive effect of productivity and disturbance. When accounting for density (rarefaction) the results were inconsistent, exhibiting no relationship with productivity but declining with disturbance. Our results suggest both the Death and Tonkin productivity-disturbance-diversity models are the most applicable in these communities where disturbance simply removes taxa and productivity controls the upper limit to richness.

**Key words:** benthic macroinvertebrates; DEM; diversity; land-use; New Zealand; productivity-disturbance-diversity relationship; species richness.

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### INTRODUCTION

The explanation of diversity patterns has been a focus for ecologists for a long time and continues to be a major challenge due to the multitude of explanatory factors (e.g., Huston 1994, Hubbell 2001, Ricklefs 2004). Consequently, rather than single factor models, ecologists have developed ever more complex models to explain diversity patterns. Mackey and Currie (2001), in their review, highlight the fact that there is an

ever lengthening list of factors that *can* influence diversity in natural systems, but there has been little progress in identifying what factors explain the majority of variation in diversity observed in nature. Emphasis has been on developing diversity models based on abiotic controls, particularly disturbance interrupting processes such as competitive exclusion. Of the many factors that have been hypothesized to determine diversity patterns in natural environments, disturbance (Connell 1978, Wootton 1998, Lake 2000) and

productivity (Currie 1991, Waide et al. 1999, Mittelbach et al. 2001) are those most often invoked. Often, the appeal of these hypotheses is their simplicity; however, this can also be their weakness as they may only apply to a single trophic level (Wootton 1998, Mackey and Currie 2001). Nevertheless, although these models appear simplistic at a glance they may in fact account for multiple underlying mechanisms of coexistence (Roxburgh et al. 2004).

Two of the most longstanding models of diversity are the Intermediate Disturbance Hypothesis (IDH) (Connell 1978) and the Dynamic Equilibrium Model (DEM) (Huston 1979, 1994). The IDH predicts diversity to peak at intermediate levels of disturbance and the DEM, and Kondoh's extension of this model (Kondoh 2001), builds on the IDH to predict a peak at intermediate levels of productivity and an interaction between disturbance and productivity. Several empirical studies have found an interaction between productivity and disturbance to be important in controlling diversity (e.g., Kneitel and Chase 2004, Death and Zimmermann 2005, Scholes et al. 2005). However, at the time of their publication Mackey and Currie (2000) found little evidence to suggest that disturbance should play more than a minor role in determining diversity patterns in nature.

There has been limited support for any of the major models of diversity in lotic systems (but see Townsend et al. 1997). However, disturbance both alone (Death and Winterbourn 1995, Lake 2000), and in combination with productivity (Death 2002, Cardinale et al. 2006), has been found to have a strong influence on diversity of stream benthic communities and is clearly one of the most important structuring forces of stream communities (Resh et al. 1988, Lake 2000, Death 2008). Yet, there is little consensus on how diversity responds to productivity and disturbance. Streams provide a unique testing ground for these models because community dynamics are influenced heavily by immigration and emigration rather than population growth alone for which most theoretical and empirical work in this field has been applied. Many of the dominant diversity models in ecology are developed for sedentary organisms such as corals and plants (e.g., IDH: Connell 1978). However, these assumptions, such as sedentary organisms, are

not often met in lotic communities which are dominated by highly mobile taxa (Hildrew and Giller 1994, Allan 1995).

Disturbance can shape local assemblages in lotic environments through many means including low-flows (Dewson et al. 2007) and man-made disturbances such as land-use change (Allan 2004); however flooding is likely the most pervasive form of physical disturbance in streams (Death 2008). Death (2002) proposed a model that, like the DEM, has diversity predicted by the interaction between productivity and disturbance. He found substrate disturbance had a considerably weaker effect on macroinvertebrate communities in forested streams where light was limiting primary productivity. He proposed that the principal effect of disturbance on diversity in New Zealand streams was to limit primary productivity. This implies that productivity sets an upper limit to invertebrate diversity in streams and disturbance resets the colonization process of stream invertebrates. This model predicts that diversity will increase log-linearly with increasing productivity and decline linearly with increasing disturbance. Tonkin et al. (2012) built on this model to suggest a quadratic decline in diversity with increasing disturbance and found a stronger dependence on productivity and disturbance in open, as opposed to closed canopy streams.

Although there is evidence of an interactive effect of productivity and disturbance on diversity in numerous ecological systems (Kneitel and Chase 2004, Scholes et al. 2005), the way in which this interaction operates to affect diversity is not clear. Cardinale et al. (2006) found evidence of this interaction when applying the DEM to a wide range of North American streams, yet when testing for this interaction on pristine New Zealand mountain streams, Tonkin et al. (2012) found no such interactive effect of productivity and disturbance on diversity. Essentially, whether the effects of productivity and disturbance on diversity are additive or multiplicative is still unclear. We would expect if productivity was controlling the rate of recolonization after disturbance that there should be significant interaction terms.

Habitats worldwide are under threat from increasing land use intensification (Tilman 1999, Allan 2004, Foley et al. 2005). Changes in land

use such as agricultural intensification can severely alter the composition and biodiversity of communities living within these landscapes (Harding et al. 1998, Allan 2004, Tschardt et al. 2005). Not only will changes in land use alter the composition of communities, but in streams, alteration of catchment land use can lead to drastic changes in the flood regime (Rowe et al. 1997, Walsh et al. 2005). Pastoral development appears to influence lotic communities through a suite of mechanisms such as changes to sediment, temperature and light regimes, channel morphology, hydrology, and the food base (Quinn 2000, Allan 2004). However, research on the influence of agricultural intensification on flood-effects is limited (Death 2008), but Collier and Quinn (2003) found that pulse disturbance, through a major catchment-scale flood, can have differential effects on forested and pasture streams. They suggest that interaction between press disturbance (land-use change) and pulse disturbance (floods) (Lake 2000) can have strong effects on the post-flood recovery of lotic communities.

While the effects of catchment land use and flow disturbance on stream invertebrate communities are well understood in isolation, the interactive effects of these two factors are not well documented. Specifically, we do not yet have a clear comprehension of how invertebrate communities respond to flooding under different land use regimes. As far as we know, no one has investigated whether varying composition of communities as a result of different land use leads to differential responses of diversity patterns to productivity and disturbance. Here we (1) investigate whether the effects of productivity and disturbance on diversity differ between a pristine and non-pristine agricultural region and (2) assess the fit of three different productivity-disturbance-diversity models in these systems by sampling 16 streams on multiple occasions in the North Island of New Zealand. In order to do this we (1) analyze differences in diversity between three factors in a factorial design - land-use, productivity and disturbance, (2) assess linear relationships between productivity, disturbance and diversity, and (3) fit these data to three models of productivity-disturbance-diversity: the DEM (Huston 1979, 1994), Death's (2002) model of diversity specifically developed for stream

communities, and Tonkin et al.'s (2012) adaptation of this model. Based on Tonkin et al. (2012) and Death (2002) we predict diversity will increase log-linearly with productivity and decline (linear or quadratic) with disturbance at pristine sites. We predict that non-pristine sites will be affected by disturbance more severely than pristine sites and diversity will decline at the higher levels of productivity. We expect the change in land-use will lead to clearer interactions between productivity and disturbance due to the more extreme effects of floods on these streams and higher productivity associated with land-use change to agriculture.

## METHODS

### *Study sites*

Eight streams were sampled in each of two regions which were selected to represent a pristine (Tongariro) and non-pristine (Hawke's Bay) region. The Tongariro National Park, in the North Island central plateau of New Zealand, is dominated by a central volcanic massif. Rainfall ranges from 1,100–3,500 mm yr<sup>-1</sup> and vegetation varies within the park from mixed beech-podocarp forest to native tussock and scrub. Pastoral farming and wine production dominates the land-use of Hawke's Bay, in the East of the North Island, which is characterized by a warm and dry climate with a mean annual rainfall of 783 mm in the central Ruataniwha Plains. Study sites were selected to represent high and low productivity in each of stable and unstable streams in the two regions. Classification of sites as high or low productivity/stability was based on visual estimates of algal cover, overhead canopy cover, conductivity and the Pfankuch bottom component (Pfankuch 1975). Fig. A1 (Appendix A) shows the location of the 16 sites in the North Island of New Zealand.

### *Sampling protocol*

Sampling took place on four occasions between February 2008 and August 2009. Two samplings took place in the austral summer and two in the austral winter in February 2008, September 2008, February 2009 and August 2009. Macroinvertebrates were sampled by taking five 0.1 m<sup>2</sup> Surber samples (250 µm mesh) from random locations in riffles throughout ~50

m reaches at each site. Samples were stored in 10% formalin and later identified in the laboratory to the lowest possible taxonomic level using available keys (e.g., Towns and Peters 1996, Winterbourn et al. 2000).

To assess primary productivity we used a measure of biomass accumulation on tiles placed on the substrate. One month prior to each of the four sampling occasions one set of six unglazed terracotta tiles were deployed at each site. Six 45 × 45 mm tiles were attached to one 500 × 500 mm interlocking rubber safety mat at each site. The six tiles were attached at evenly spaced intervals on the mats by drilling 10 mm holes in tiles and mats and attaching via 10 mm dowell. Mats were secured in place flush with the streambed with a metal fencing pole and long tent pegs. These mats were left in place for one month prior to sampling.

As a second estimate of primary productivity we also measured biomass on natural substrates at each site by extracting chlorophyll *a*. While there are caveats involved in this estimation such as different rates of grazing pressure, periphyton chlorophyll *a* and primary productivity in streams are highly correlated; Morin et al. (1999), in an extensive review, found a strong log-linear relationship ( $r^2 = 0.63$ ) between the two. Five stones ( $\alpha$  axis < 60 mm) were randomly collected from each riffle for extraction of chlorophyll *a*. Stones and tiles were kept cool and dark on ice in the field before being stored at -20°C. Photosynthetic pigments were extracted from stones or tiles by submerging in known volumes of 90% acetone for 24 hours at 5°C. Absorbances at 750, 665 and 664 nm were read on a Varian Cary 50 conc UV-Visible Spectrophotometer (Varian Australia Pty Ltd, Mulgrave, Australia) and converted to chlorophyll *a* and phaeophytin pigment concentration using Steinman and Lamberti (1996). These were then corrected for stone surface area using Graham et al. (1988) and halved to account for periphyton being present only on exposed surfaces.

#### *Measurement of disturbance*

We measured disturbance as physical disturbance of the substrate through flooding due to this being the most dominant form of disturbance in lotic systems (Lake 2000). Bed stability/substrate disturbance was assessed using the

Pfankuch stability index (Pfankuch 1975). Only the bottom component of the index (which evaluates rock angularity, brightness, packing, percent stable materials, scouring, and amount of clinging vegetation) was used, as this is more relevant to stream invertebrate communities (Death and Winterbourn 1994). We supplemented this with direct measurement of stone movement at the streams.

Fifteen stones were used at each site, five from each of three size classes were placed in sets of three (one of each of the three size class) at equidistant intervals along the study reach (up to 100 m). Stones were selected from the  $D_{50}$ ,  $D_{70}$  and  $D_{90}$  of individual streams. Stones at each stream were marked with fluorescent spray paint before being placed in the bed. These tracer particles were placed in the bed as closely mimicking the surrounding stones as possible without unnecessary disturbance of the bed (i.e., embedded or sitting loosely). Rather than measure distances moved by individual tracers as previous studies have (e.g., Downes et al. 1998, Death and Zimmermann 2005), stones were simply recorded as moved or not, similar to that of Townsend et al. (1997). Distances moved were not recorded because disturbance relevant to benthic invertebrates is indicated by whether the substrate is entrained or not, and not by how far particles move. Nonetheless, magnitude was somewhat accounted for by using three size classes of substrate, and thus an index of bed movement is simply the percentage of overall stone movement for each stream. Stone movement was measured for the month leading up to biological sampling.

#### *Other environmental measures*

To ensure treatments did not fundamentally differ in physicochemical characteristics and to explore other potential influences on patterns found in these systems, we measured several physicochemical variables. 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 propor-



tion. Bedrock was assigned a nominal size of 400 mm. Conductivity, temperature and pH were measured using ECScan pocket meters. Depth and velocity were recorded with a Marsh-McBirney flowmate current meter in the thalweg of each stream at five points at equidistant intervals along the study reach. Flow type of each site was assessed visually as percentage of still, backwater, pool, run or riffle over a 100 m reach. Percentage of leaf litter, riparian vegetation and canopy cover were also visually assessed.

### Community metrics

The number of individuals and two simple measures of diversity were used in this study: the number of taxa (richness) and rarefied species richness (ESN). Rarefaction accounts for the likelihood of capturing rare taxa with increased number of individuals collected (Hurlbert 1971). This is achieved by standardizing the sites by predicting the number of taxa expected for a fixed number of individuals. In order to get sufficient numbers for the index to be accurate the five replicates at each site were pooled to give one value for each site. Five site samplings were removed because of the low number of collected animals and rarefied richness was calculated for 224 individuals.

### Statistical analysis

The effects of productivity, stability and region based on a priori group selection were assessed using three-way crossed Analysis of Variance (ANOVA) design in Statistix (Statistix 8, Analytical Software, Tallahassee, FL, USA). All possible interactions were included and seasonal samples were included as replicates. All three factors were treated as fixed. Where required data were  $\log(x + 1)$  transformed in order to normalize the data. To assess whether there were in fact differences in the taxa found in each region and community structure between the two regions and two treatments, we carried out a non-metric multi dimensional scaling (NMDS) ordination on  $\log(x + 1)$  data using Bray-Curtis similarity and tested for significance using analysis of similarities (ANOSIM) (Clarke 1993) in Primer v6 (Clarke and Gorley 2006).

Regression analysis was used to explore relationships between productivity, disturbance and diversity also using Statistix. Akaike's

Information Criterion (Akaike 1974) was used to determine the best fitting curve to the data when two models fit the data equally. This method takes into account goodness of fit statistics and the number of parameters involved in the fitting of the model to select the model most preferred. We then explored the fit of our data to three main models (and two sub-models) of diversity in relation to productivity and disturbance. These models are the Dynamic Equilibrium Model (Huston 1979, 1994) modified by Kondoh to account for meta-population dynamics (Kondoh 2001), the Death (Death 2002) productivity-disturbance-diversity model, and a model suggested by Tonkin et al. (2012) which adds to that of Death (2002) by including a quadratic factor between disturbance and diversity. The five models tested using multiple regression are of the following forms:

Eq. 1. DEM

$$S = b_0 + b_1D + b_2C + b_3D^2 + b_4C^2 + b_5D \times C$$

Eq. 2. Death model without interaction between productivity and disturbance

$$S = b_0 + b_1D + b_2[\ln(C)]$$

Eq. 3. Death model with interaction between productivity and disturbance

$$S = b_0 + b_1D + b_2[\ln(C)] + b_3D \times C$$

Eq. 4. Tonkin model without interaction between productivity and disturbance

$$S = b_0 + b_1D + b_2[\ln(C)] + b_3D^2$$

Eq. 5. Tonkin model with interaction between productivity and disturbance

$$S = b_0 + b_1D + b_2[\ln(C)] + b_3D^2 + b_4D \times C$$

where  $D$  = disturbance (percent tracer particle movement),  $C$  = chlorophyll  $a$  ( $\mu\text{g cm}^{-2}$ ),  $S$  = number of taxa, and  $b_0$ – $b_5$  = regression coefficients. In models 1, 3 and 5 the interaction between productivity and disturbance has been included. Significance of this term indicates whether the two interact to affect diversity. That is, whether the multiplicative effects of productivity and disturbance is stronger than the simple addition of the two regression models. AIC was used to assess the best fitting models.

## RESULTS

### *Physical characteristics and disturbance*

Tongariro streams were on average slightly deeper, faster and wider than Hawke's Bay streams (Appendix B: Table B1). Hawke's Bay streams had higher conductivity (mean: Hawke's Bay =  $137.5 \mu\text{S cm}^{-1}$ , Tongariro =  $98.8 \mu\text{S cm}^{-1}$ ) and temperature (mean: Hawke's Bay =  $14^\circ\text{C}$ , Tongariro =  $8.8^\circ\text{C}$ ) than Tongariro streams. Little differences in physicochemical variables were evident between both a priori high and low productivity groups and stable and unstable groups (Appendix B: Table B1).

There was on average only 14.6% movement at stable sites compared to 45.8% at unstable sites ( $F_{1,59} = 12.49$ ,  $P = 0.0008$ ). Hawke's Bay streams had greater overall movement (41.1%) compared to Tongariro streams (21%) ( $F_{1,59} = 4.5$ ,  $P = 0.038$ ). There was no difference in artificial substrate movement between season ( $F_{3,59} = 1.37$ ,  $P = 0.26$ ). Overall, measurements of substrate movement correlated well with the bottom component of the Pfankuch index ( $r = 0.57$ ). Bed movement will hereafter be used as the measure of disturbance for the remainder of the analysis.

### *Periphyton*

Of the 16 sites and 63 sets of tiles, 32 sets of tiles remained for assessment, the others either being washed away or shaded by macrophytes. Periphyton biomass on stones was highly correlated to periphyton biomass on tiles ( $r = 0.86$ ,  $P < 0.0001$ ). We therefore used chlorophyll *a* from stones as a surrogate for productivity. Periphyton biomass, assessed as chlorophyll *a*, ranged from  $0.01 \mu\text{g cm}^{-2}$  to  $12.2 \mu\text{g cm}^{-2}$  at all sites. Periphyton biomass, not surprisingly, was higher at high ( $1.46 \mu\text{g cm}^{-2}$ ) than low productivity sites ( $0.62 \mu\text{g cm}^{-2}$ ) ( $F_{1,61} = 5.28$ ,  $P = 0.025$ ). Overall periphyton biomass did not differ between regions ( $F_{1,59} = 0.15$ ,  $P = 0.7$ ). However, periphyton biomass was significantly higher at stable streams ( $1.40 \mu\text{g cm}^{-2}$ ) than unstable streams ( $0.70 \mu\text{g cm}^{-2}$ ) ( $F_{1,59} = 5.32$ ,  $P = 0.02$ ). There was no interaction between region and stability ( $F_{1,59} = 0.28$ ,  $P = 0.6$ ) (Fig. 1). Periphyton biomass declined with increasing bed disturbance (Fig. 1, Table 1). This trend was stronger at Hawke's Bay sites compared to Tongariro sites but the trend was the same.

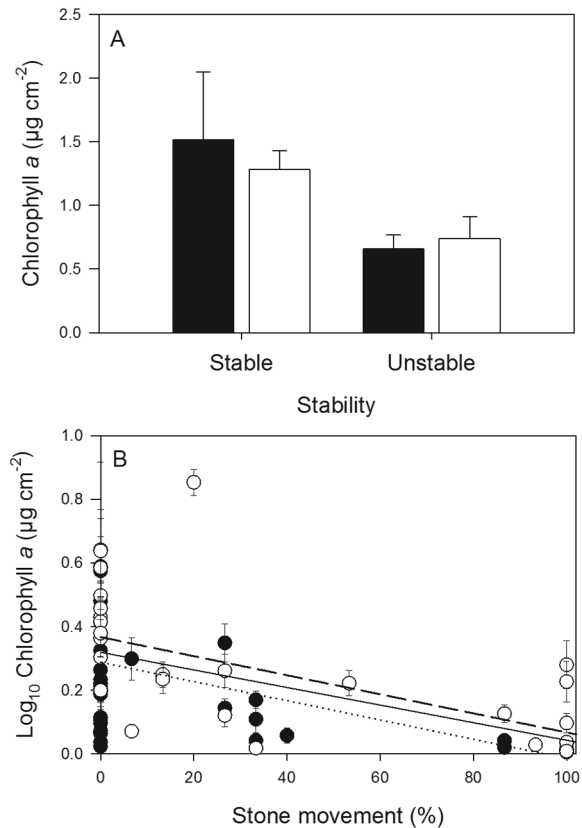


Fig. 1. Mean chlorophyll *a* concentrations ( $\pm 1$  SE) (a) for sites in each a priori selected stability group in both regions and (b) as a function of percent stone movement collected in 16 streams, North Island, New Zealand, February 2008–July 2009. Black bars/circles are pristine (Tongariro) and open bars/circles are non-pristine (Hawke's Bay). Solid line = all sites, dashed line = non-pristine sites and dotted line = pristine sites. See text for ANOVA results and Table 1 for regression results.

### *Community composition*

One hundred and eleven taxa were collected from all sites in this study. Although the Hawke's Bay sites had more than twice the number of collected animals (93,609) to that of the Tongariro sites (40,570), 23 more taxa were collected from Tongariro (97) than in Hawke's Bay (74). Insect taxa dominated invertebrate communities in both regions. Ephemeroptera (16.5%), Trichoptera (28.8%) and Diptera (28%) made up 73.4% of all animals collected. This structure was slightly different between the two regions with 67.8% insects in Hawke's Bay and 86.2% in Tongariro.

Table 1. Results of regression analysis of chlorophyll *a* and three invertebrate community metrics against (a) % stone movement and (b) chlorophyll *a* collected in 16 North Island, New Zealand streams on four occasions between February 2008 and July 2009.

Variable	df	F (AIC)	P	r <sup>2</sup>	Equation
a) % moved					
Chlorophyll <i>a</i>	1, 61	20.1	<0.0001	0.25	$y = 0.32 - 0.0028x$
Pristine	1, 30	6.81	0.014	0.19	$y = 0.29 - 0.003x$
Non-pristine	1, 29	19.28	0.0001	0.4	$y = 0.37 - 0.003x$
No. of individuals	1, 61	19.49 (-31.01)	<0.0001	0.24	$y = 2.53 - 0.007x$
Quadratic	2, 60	10.55 (-29.67)	0.0001	0.26	$y = 2.49 + 0.002x - 0.00009x^2$
Pristine	1, 30	23.04	<0.0001	0.43	$y = 2.33 - 0.012x$
Non-pristine	1, 29	19.65	0.0001	0.4	$y = 2.76 - 0.007x$
No. of taxa	1, 61	33.01 (-93.91)	<0.0001	0.35	$y = 1.26 - 0.003x$
Quadratic	2, 60	19.71 (-93.90)	<0.0001	0.4	$y = 1.23 + 0.002x - 0.00005x^2$
Pristine	1, 30	18.60	0.0002	0.38	$y = 1.25 - 0.0045x$
Non-pristine	1, 29	37.86	<0.0001	0.57	$y = 1.27 - 0.0024x$
Rarefied richness	1, 56	5.92	0.018	0.1	$y = 19.6 - 0.04x$
Pristine	1, 26	0.04	0.84	0.002	Non-significant
Non-pristine	1, 28	5.15	0.03	0.16	$y = 17.55 - 0.03x$
b) Periphyton biomass					
No. of individuals	1, 61	67.98	<0.0001	0.53	$y = 2.98 + 0.32 \cdot \ln(x)$
Pristine	1, 30	34.66	<0.0001	0.53	$y = 2.83 + 0.35 \cdot \ln(x)$
Non-pristine	1, 29	84.44	<0.0001	0.74	$y = 3.14 + 0.29 \cdot \ln(x)$
No. of taxa	1, 61	48.64	<0.0001	0.44	$y = 1.38 + 0.1 \cdot \ln(x)$
Pristine	1, 30	26.67	<0.0001	0.47	$y = 1.44 + 0.13 \cdot \ln(x)$
Non-pristine	1, 29	32.96	<0.0001	0.53	$y = 1.32 + 0.07 \cdot \ln(x)$
Rarefied richness	1, 56	0.09	0.76	0.002	Non-significant
Pristine	1, 26	0.02	0.9	0.0006	Non-significant
Non-pristine	1, 28	0.98	0.33	0.03	Non-significant

Notes: df = degrees of freedom. AIC = Akaike's information criterion where lower numbers represent a better model.

Unstable sites were dominated by the mayfly *Deleatidium* spp. averaging 47.3% at unstable-low productivity sites and 21.1% at unstable-high productivity sites. Stable-low productivity sites were dominated by molluscan taxa (25.8%) and oligochaetes (18.5%).

Community structure differed between the two regions ( $R = 0.42$ ,  $P = 0.001$ ; Appendix C: Fig. C1), and using presence/absence data suggested it was not only abundances that were different but also composition of species ( $R = 0.47$ ,  $P = 0.001$ ). The greatest variation in densities between communities occurred within the pristine unstable sites (avg. similarity: 35.9) whereas non-pristine unstable sites were more similar (avg. similarity: 48.7). Non-pristine stable sites had the most similar communities (avg. similarity: 52.6; pristine stable avg. similarity: 43.2). No single taxon contributed more than 5.6% to the difference between communities between the regions. Of the most important taxa, *Pycnocentroides aeris*, *Deleatidium* spp., *Oligochaeta*, *Potamopyrgus antipodarum* and *Paracalliope fluviatilis* were more prevalent in Hawke's Bay streams whereas *Maoridiamesa* spp., two orthoclad chironomids, *Zelandoperla* spp. and *Hydora* spp.

were more abundant in Tongariro. Although the difference in community structure was greatest between regions, it also differed between stable and unstable sites ( $R = 0.16$ ,  $P = 0.001$ ) and less so between low and high productivity sites ( $R = 0.06$ ,  $P = 0.017$ ; Appendix C: Fig. C1). However, community dissimilarities with both stability and productivity were due primarily to differences in relative abundances of dominant taxa rather than changes in composition. *Deleatidium* spp., a species of Orthoclaadiinae, *Maoridiamesa* spp., and the cased caddisfly *Pycnocentroides aeris* contributed to 16.4% of the difference between stable and unstable sites and 17.7% between low and high productivity sites. All of these taxa were higher at high productivity sites and, barring *Deleatidium* spp., higher at stable sites.

#### Density and diversity

The density of invertebrates per 0.1 m<sup>2</sup> was significantly higher at Hawke's Bay streams with 603.93 individuals 0.1 m<sup>-2</sup> opposed to Tongariro's 253.58 individuals 0.1 m<sup>-2</sup> (Table 2). Density was significantly higher at stable than unstable streams, with 578.63 individuals 0.1 m<sup>-2</sup> at stable

Table 2. Three-way ANOVA results testing for differences in mean number of animals, mean number of taxa, and rarefied number of taxa between region and a priori stability and productivity groups collected in 16 North Island, New Zealand streams on four occasions between February 2008 and July 2009.

Factor	No. animals		No. taxa		Rarefied richness (ES224)	
	F	P	F	P	F	P
Stability	18.19	0.0001	28.81	<0.0001	5.89	0.018
Productivity	13.69	0.0005	15.32	0.0003	0.28	0.6
Region	18.93	0.0001	0.17	0.68	11.58	0.001
Stability $\times$ productivity	7.79	0.007	11.31	0.001	3.91	0.053
Stability $\times$ region	0.38	0.54	1.95	0.17	2.37	0.13
Productivity $\times$ region	3.53	0.065	0.96	0.33	1.59	0.21
Stability $\times$ productivity $\times$ region	0.81	0.37	7.05	0.01	10.51	0.002

streams and 278.1 individuals  $0.1 \text{ m}^{-2}$  at unstable streams but there was no interaction between stability and region. Density was significantly higher at high productivity sites with 515.8 individuals and 333.2 individuals at low productivity sites. There was no interaction between productivity and stability nor was there a three way interaction including region. Density increased logarithmically with increasing periphyton biomass and declined with increasing bed movement (Fig. 2, Table 1). These relationships were the same for both regions. However when fitted individually, slight differences in the curves meant each model explained a greater proportion of the variation in the data (Fig. 2, Table 1).

The mean number of taxa per sample at each site (richness) was slightly higher on average in Tongariro streams with 15.49 taxa  $0.1 \text{ m}^{-2}$  and 14.57 taxa  $0.1 \text{ m}^{-2}$  at Hawke's Bay streams; however, this was not a significant difference (Table 2). Richness was higher at stable sites with 18.11 taxa  $0.1 \text{ m}^{-2}$  and 12.07 taxa  $0.1 \text{ m}^{-2}$  at unstable sites. Richness was higher at high productivity sites with 17 taxa and 13 at low productivity sites. Productivity and stability interacted to effect richness and there was also a three-way interaction between productivity, stability and region. Taxonomic richness increased logarithmically with increasing periphyton biomass and declined with decreasing bed stability (Fig. 2, Table 1). These trends were consistent for both regions but the fit of both models was greater at Hawke's Bay sites.

Rarefied taxa richness, pooled for 224 individuals was higher at Tongariro streams with 20.74 taxa at these streams and 16.41 taxa at Hawke's Bay streams (Table 2). Rarefied richness was higher at stable sites (19.71) than at unstable sites

(16.89), but there was no difference between high and low productivity groups. There was no interaction between region and stability, but productivity and stability did interact with region. Rarefied richness declined gradually with increasing bed movement (Fig. 2, Table 1). When fitting to each individual region, no relationship was found between bed movement and rarefied richness at Tongariro sites. There was no relationship between periphyton biomass and rarefied richness at all sites.

#### Model fitting

All five models explained a large proportion of the variation in taxonomic richness at all sites (Fig. 3, Table 3, Appendix D: Table D1). The DEM explained 50.9 % of the variation in the data for the number of taxa (Fig. 3, Table 3). The Tonkin model explained the most variation in the data with 52.4% when the interaction between productivity and disturbance was included and 51.9% without the interaction. The Death model explained 47.9% of the variation with and without the interaction between productivity and disturbance included. Akaike's information criterion shows that the Tonkin and Death models without interaction are the best models based on a trade-off between simplicity and fit statistics. The difference between the two AIC values is negligible and thus we can consider these two equally well fitting. Our model fitting shows that there is no interaction between the way productivity and disturbance effect richness, thus the effect of productivity and disturbance on diversity in these streams is additive rather than multiplicative. The only model of the five to have every coefficient significantly affecting richness is the Death model without interaction (Fig. 3,



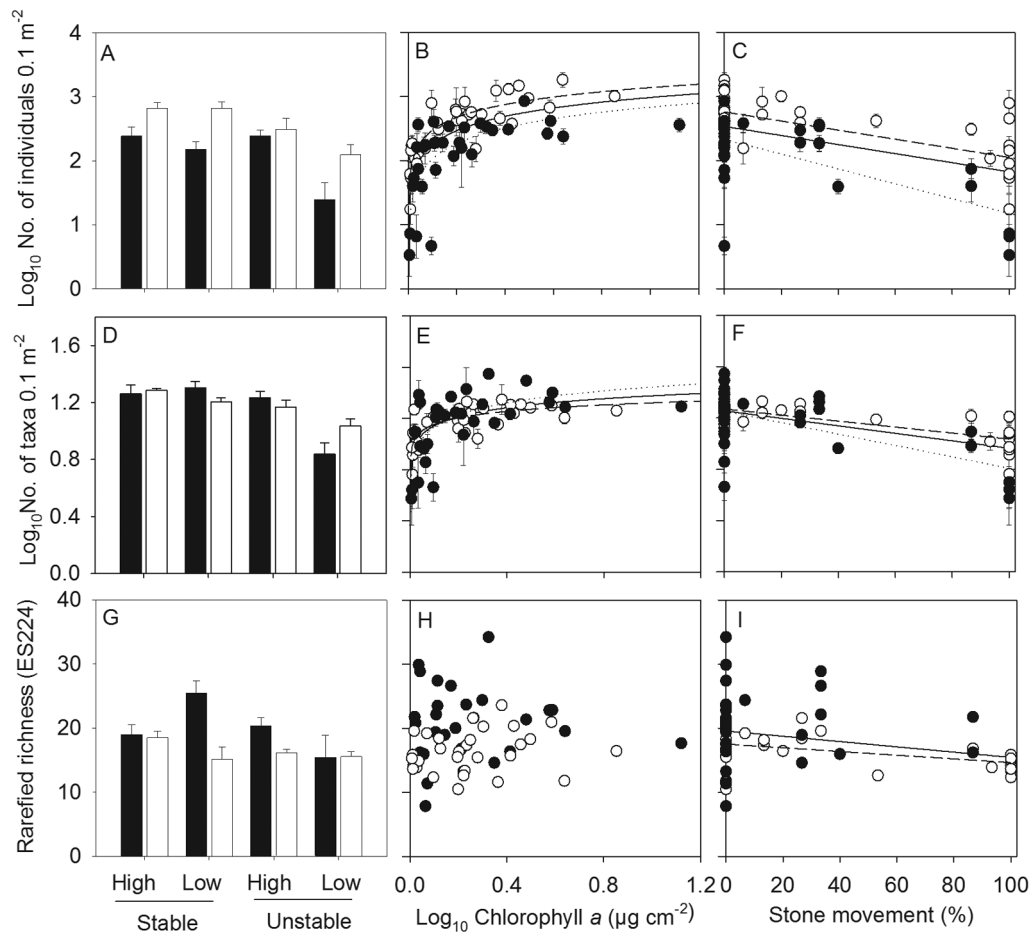


Fig. 2. Mean ( $\pm 1$  SE) (a, b, c) number of animals, (d, e, f) number of taxa, and (g, h, i) rarefied richness collected in 16 North Island, New Zealand streams on four occasions between February 2008 and July 2009. (a, d, g) For each a priori selected stability and productivity group, (b, e, h) as a function of mean chlorophyll *a* and (c, f, i) as a function of percent stone movement. For regressions, number of animals and number of taxa are means and rarefied richness is calculated for pooled total per site. Black bars/circles are pristine (Tongariro) and open bars/circles are non-pristine (Hawke's Bay). Solid line = all sites, dashed line = non-pristine sites and dotted line = pristine sites. See Table 2 for ANOVA results and Table 1 for regression results.

Appendix: Table D1). The productivity coefficients were significant throughout all five models whereas the only significant disturbance coefficients were the disturbance<sup>2</sup> coefficients. Although the DEM explains more than the Death model, due to the complexity of the model it results as the worst model for the data (Fig. 3, Table 3). Although the Death model explains the least amount of variation in the data, the difference between the amount of variation explained by all five models is small ( $0.48 < r^2 < 0.52$ ).

When fitting the models to each individual region, the Death and Tonkin models without the interaction term were the most applicable in both regions (Fig. 3, Table 3). However, model fit was consistently better in the non-pristine sites than the pristine sites. Although the DEM did explain a large proportion of the variation, AIC indicated it was the least likely model for these data. Each of the three models with the productivity-disturbance interaction fit differently to the pristine sites (Fig. 3). The two models with the interaction and a quadratic relationship between

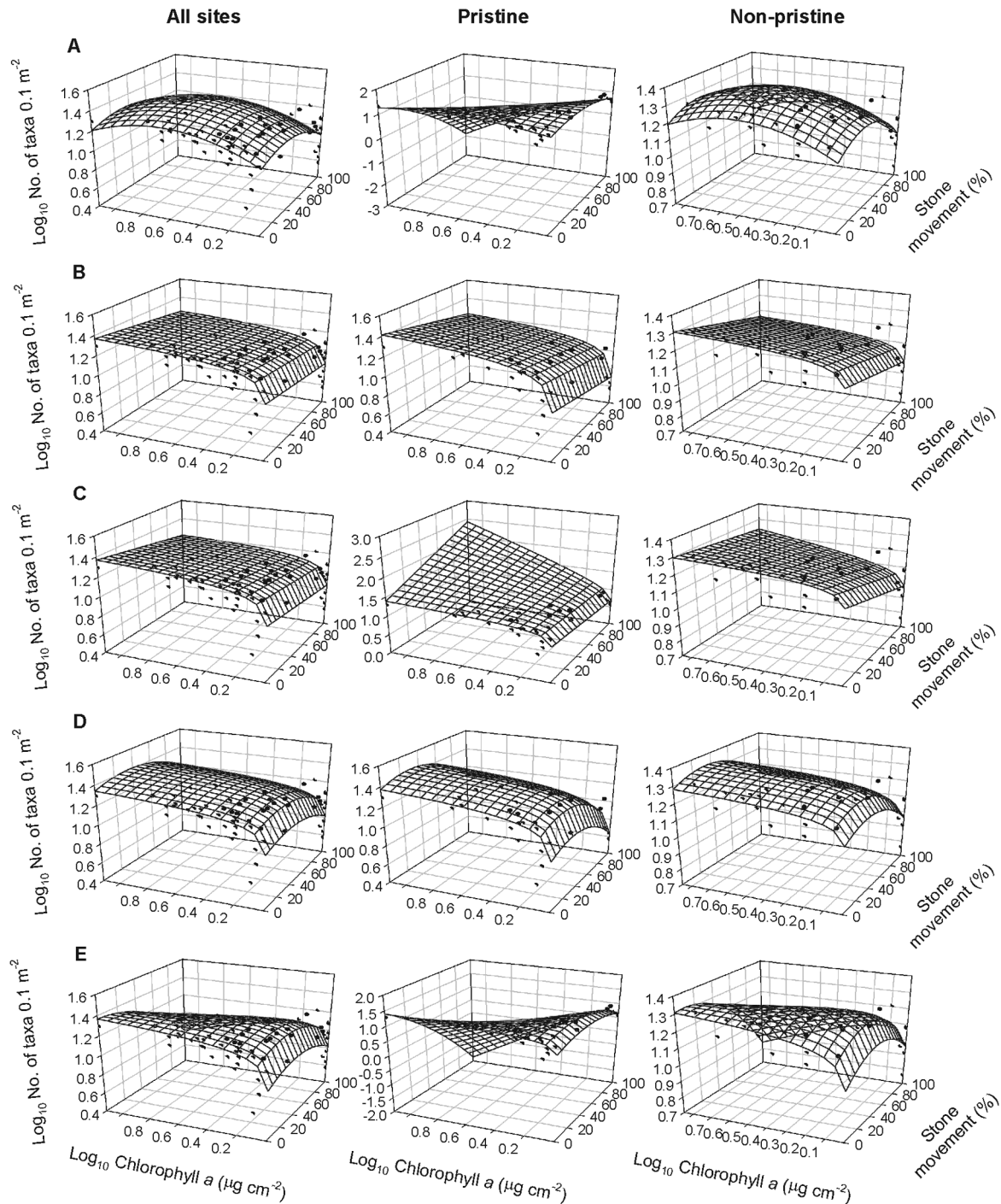


Fig. 3. Model fit for mean number of taxa collected from 16 North Island, New Zealand sites on four occasions between February 2008 and July 2009 with all sites included, pristine only (Tongariro) and non-pristine only (Hawke's Bay) sites. (a) DEM, (b) Death model, no  $P \times D$  (productivity  $\times$  disturbance) interaction; (c) Death model, with  $P \times D$  interaction; (d) Tonkin model, no  $P \times D$  interaction; and (e) Tonkin model, with  $P \times D$  interaction. See Table 3 for model fit results and Appendix D: Table D1 for model coefficients.

Table 3. Model fit results for five models predicting mean number of taxa collected from 16 North Island, New Zealand sites on four occasions between February 2008 and July 2009 with (a) all sites included, (b) pristine only (Tongariro) and (c) non-pristine only (Hawke's Bay) sites.

Model	df	F	P	RMSE	$r^2$	AIC
a) All sites						
DEM	5, 57	11.82	<0.0001	0.15	0.51	-93.55
Death	2, 60	27.55	<0.0001	0.15	0.48	-97.90
Death (with interaction)	3, 59	18.06	<0.0001	0.15	0.48	-95.91
Tonkin	3, 59	21.17	<0.0001	0.14	0.52	-98.07
Tonkin (with interaction)	4, 58	15.98	<0.0001	0.14	0.52	-96.41
b) Pristine						
DEM	5, 26	7.71	0.0001	0.17	0.60	-37.68
Death	2, 29	14.89	<0.0001	0.18	0.51	-40.86
Death (with interaction)	3, 28	9.85	0.0001	0.18	0.51	-39.05
Tonkin	3, 28	12.08	<0.0001	0.17	0.56	-40.58
Tonkin (with interaction)	4, 27	9.40	<0.0001	0.17	0.58	-39.17
c) Non-pristine						
DEM	5, 25	11.58	<0.0001	0.08	0.70	-55.53
Death	2, 28	24.71	<0.0001	0.09	0.64	-59.08
Death (with interaction)	3, 27	15.97	<0.0001	0.09	0.64	-57.13
Tonkin	3, 27	21.49	<0.0001	0.08	0.70	-59.82
Tonkin (with interaction)	4, 26	16.51	<0.0001	0.08	0.72	-58.41

Notes: With interaction indicates the productivity  $\times$  disturbance interaction term is included in the model. RMSE = root mean square error. AIC = Akaike's information criterion where lower numbers represent a better model.

disturbance and diversity suggested diversity at the pristine sites would decline significantly at high levels of disturbance and productivity.

## DISCUSSION

Diversity of invertebrate communities was strongly related to both productivity and disturbance in this study. We found evidence to support Death's (2002) productivity-disturbance-diversity model in these streams, as well as Tonkin et al.'s (2012) modification of this model to include a quadratic disturbance-diversity relationship. Huston's (1979, 1994) DEM received the least support of the three models applied to these streams. There was little difference in the way in which productivity and disturbance affected diversity between the pristine and non-pristine regions. Not one of the models exhibited a significant interactive effect of productivity and disturbance. There was no evidence of competitive exclusion in these streams with diversity increasing and tapering with increasing productivity. This is a phenomenon widely found in lotic environments with productivity setting the upper limit to carrying capacity in streams (Death 2010).

Although the composition and density of the benthic communities differed strongly between the pristine (Tongariro) and non-pristine

(Hawke's Bay) regions, the effects of productivity and disturbance on diversity remained similar between the two regions. However, the productivity-disturbance-diversity relationship was stronger at non-pristine than pristine sites. Taxonomic richness was not affected by region but there was a significant three-way effect of productivity, disturbance and region. Changes in land use from forested to pastoral grazing can have several effects such as changes to hydrology, sediment, channel morphology, light availability (and the resulting food base shift) and temperature (Quinn 2000, Allan 2004). Changes in catchment land use can lead to flow on effects such as severe changes to flood regimes resulting from urbanization (Walsh et al. 2005) and increased peak flows during flood events resulting from deforestation (Rowe et al. 1997). When investigating a one-in-28-year flood, Collier and Quinn (2003) found flood disturbance can lead to differential effects between pastoral and forested streams. They found that although richness and density at the pasture site exhibited a delayed response compared to the forested site, community structure at the pasture site alone was destabilized by the flood. They suggest that the differential response of the two sites was due to the presence of an underlying press disturbance (land use) at the pasture site, but without replication they could not confirm whether it

was simply individual site differences. In contrast, communities in the unstable-pristine sites in our study were the least similar rather than pastoral sites. The large scale of disturbance in the study of Collier and Quinn (2003) which left few colonists available post-disturbance, makes comparing our results with those found in their study impractical.

Not only can changes in land use alter the composition of communities within these landscapes (Harding et al. 1998, Allan 2004, Tschamntke et al. 2005), but local inter-species interactions are limited by larger scale processes such as the availability of colonists and dispersal abilities. Thus, although the colonist pool is likely to be different between the two regions, the relationship between invertebrate communities and productivity and disturbance was similar between the pristine and non-pristine regions. Several studies have suggested that local diversity-productivity relationships could be heavily influenced by dispersal and colonization processes at a regional scale which may in turn generate local processes such as competition (Loreau et al. 2001, Cardinale et al. 2005). The only exception to this was the differential effects of bed movement on rarefied richness between the two regions with no link evident at pristine sites. Being part of a braided river deposit system, substrate in the Hawke's Bay was less embedded and thus diversity may have been affected more than the measured movement indicates.

Although the Death (2002) productivity-disturbance-diversity model explained the least amount of variation in the data, it was also the most simplistic and thus is favorable to the more complex DEM. There was only a small difference in predictive ability between all three models. Moreover, the model without the interaction term was the only model with all coefficients statistically significant. While our data fit slightly better to the model of Tonkin et al. (2012), the difference in strength of fit was negligible. The only difference between the models put forward by Death (2002) and Tonkin et al. (2012) is the relationship between disturbance and diversity: Death's model advocates for a linear decline in diversity rather than the quadratic of Tonkin et al.. If the quadratic relationship between disturbance and diversity was of a unimodal form in the model of Tonkin et al. (2012) we could

postulate competitive exclusion was occurring but this was not the case. Similarly, there was no decline in diversity at extremely stable sites as would be the case with the DEM. Although the IDH is one of the most widely researched patterns in ecology (e.g., England et al. 2008, Bongers et al. 2009), the unimodal relationship between disturbance and diversity is rare in nature (Mackey and Currie 2001). Likewise, there has been limited support of this unimodal trend in lotic systems but Townsend et al. (1997) found diversity peaked at intermediate levels of disturbance in South Island New Zealand streams. Svensson et al. (2007) found support for the IDH when testing the DEM but found no change in the effect of the IDH through multiple levels of productivity. Death and Winterbourn (1995) found that stream invertebrate diversity declined with disturbance irrespective of productivity.

Like Tonkin et al.'s (2012) study on the disturbance-productivity-diversity relationship, this study is also limited by a low range of sampled productivity, however there is still a clear linear decline in periphyton biomass with disturbance. Scholes et al. (2005) mentioned the importance of sampling adequate ranges of productivity and disturbance in tests of this nature in order to fully evaluate the effects operating. Death (2002) also found a clear effect of disturbance within a small range of periphyton biomass. If, however, higher levels of periphyton biomass were present we might speculate that diversity may have declined at greater levels as has been found in numerous other cases (Rosenzweig 1995, Waide et al. 1999, Mittelbach et al. 2001). However, this is dependent on competitive exclusion operating which as previously discussed is not likely in these streams. Tonkin et al. (2012) also found this log-linear increase but this was only evident at open canopy streams within the Tongariro National Park suggesting productivity is setting the upper limit to diversity in these streams.

Based on model selection, the DEM was the least applicable model to these stream communities. The DEM has received limited support in lotic systems (but see Cardinale et al. 2006). The lotic environment presents a highly open system which leads to community dynamics heavily influenced by immigration and emigration through invertebrate drift and faunas dominated



by highly mobile taxa as opposed to many other habitats being controlled by population growth through reproduction (Brittain and Eikeland 1988, Mackay 1992). This is where the DEM has limited applicability in stream communities. The DEM predicts that at high productivity/resource levels the competitive dominant will monopolize resources through increased reproduction. However in streams, immigration will be greater than emigration and thus diversity will simply increase (Death 2002). We found this here with diversity increasing to a point and then leveling off with increasing productivity. Essentially high resource levels are lowering the immigration to emigration rate rather than causing competitive exclusion as would be the case if the DEM were operating. As discussed by Death (2002), productivity is setting the upper limit for the carrying capacity of the stream, rather than leading to competitively dominant taxa excluding other less competitive taxa. For the DEM to be applicable to these streams, extinction rates would have to outweigh immigration rates during recolonization (Petraitis et al. 1989).

Disturbance not only acts by direct removal of invertebrates but by the removal of periphyton, a major component of the food web and potentially the main food base of stream food webs (Robinson and Minshall 1986, Death 2002, Death and Zimmermann 2005). In fact, this removal of periphyton may be more important than the removal of invertebrates themselves as the recolonization of invertebrates is dependent on the resources present at a site. We have found that productivity and disturbance do indeed explain a large portion of the variation in diversity, however, like Tonkin et al. (2012) we did not find any evidence that these two factors are interacting. These interactive effects of productivity and disturbance have been found in streams (e.g., Cardinale et al. 2006), however, what we found is that the effects of productivity and disturbance were additive rather than multiplicative. Perhaps the lack of interaction is indicative of the fact that models predicting interactive effects of productivity and disturbance are reliant on disturbance disrupting biotic processes such as competitive exclusion which we do not believe are occurring here. Although the inclusion of the interaction term between productivity and disturbance in the Death and

Tonkin models revealed interesting changes, they were not significant and only improved model fit moderately, if at all.

Both the number of taxa and the total number of animals were highly correlated and followed the same trends of log-linear increase with increasing periphyton and linear decline with increasing disturbance. This suggests that the number of taxa collected may simply be a function of the number of animals collected. We found that when density was accounted for in the assessment of richness, the relationship between richness and productivity disappears. However, rarefied richness still declined with increasing disturbance. Previous studies have found rarefied richness patterns to operate differently to simple richness measures. Death and Zimmermann (2005) found that rarefied richness declined with increasing disturbance and Death (2002) found lower rarefied richness at more disturbed streams. Conversely, McCabe and Gotelli (2000) found higher rarefied species richness at more disturbed experimental treatments as opposed to the number of species being lower at these treatments. The lack of relationship between rarefied richness and productivity suggests that although resources may be greater at higher productivity sites leading to a higher density of animals, this does not necessarily mean that the diversity of resources has increased and opened up new habitat for new taxa. More resources will likely lead to more individuals per species while more taxa are likely to appear when there is greater resource diversity rather than a greater volume of resources.

We have shown that a model predicting a log-linear increase in diversity with productivity and either a linear or quadratic decline with disturbance to be highly applicable to predicting diversity (Death 2002, Tonkin et al. 2012). The DEM received the least support of the three models tested in this study (Huston 1979, 1994), and there was no evidence in this study of competitive exclusion as required by the DEM. The number of taxa did not decline at higher levels of periphyton nor did it at higher stability sites. We found that the productivity-disturbance-diversity relationship was similar between pristine and non-pristine regions even though community composition differed between the regions. The main differences found were the

productivity-disturbance-diversity relationship was stronger at non-pristine sites and communities at unstable sites were more variable within a pristine as opposed to anthropogenically impacted landscape. Despite research suggesting disturbance operates on stream communities both through direct impact on animals and their resource supply, we found their effects on diversity, although strong, to be additive rather than multiplicative. We suggest both the Death (2002) model and Tonkin et al. (2012) model are applicable to ecological communities with highly mobile animals irrespective of the landscape they are applied within.

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## SUPPLEMENTAL MATERIAL

## APPENDIX A

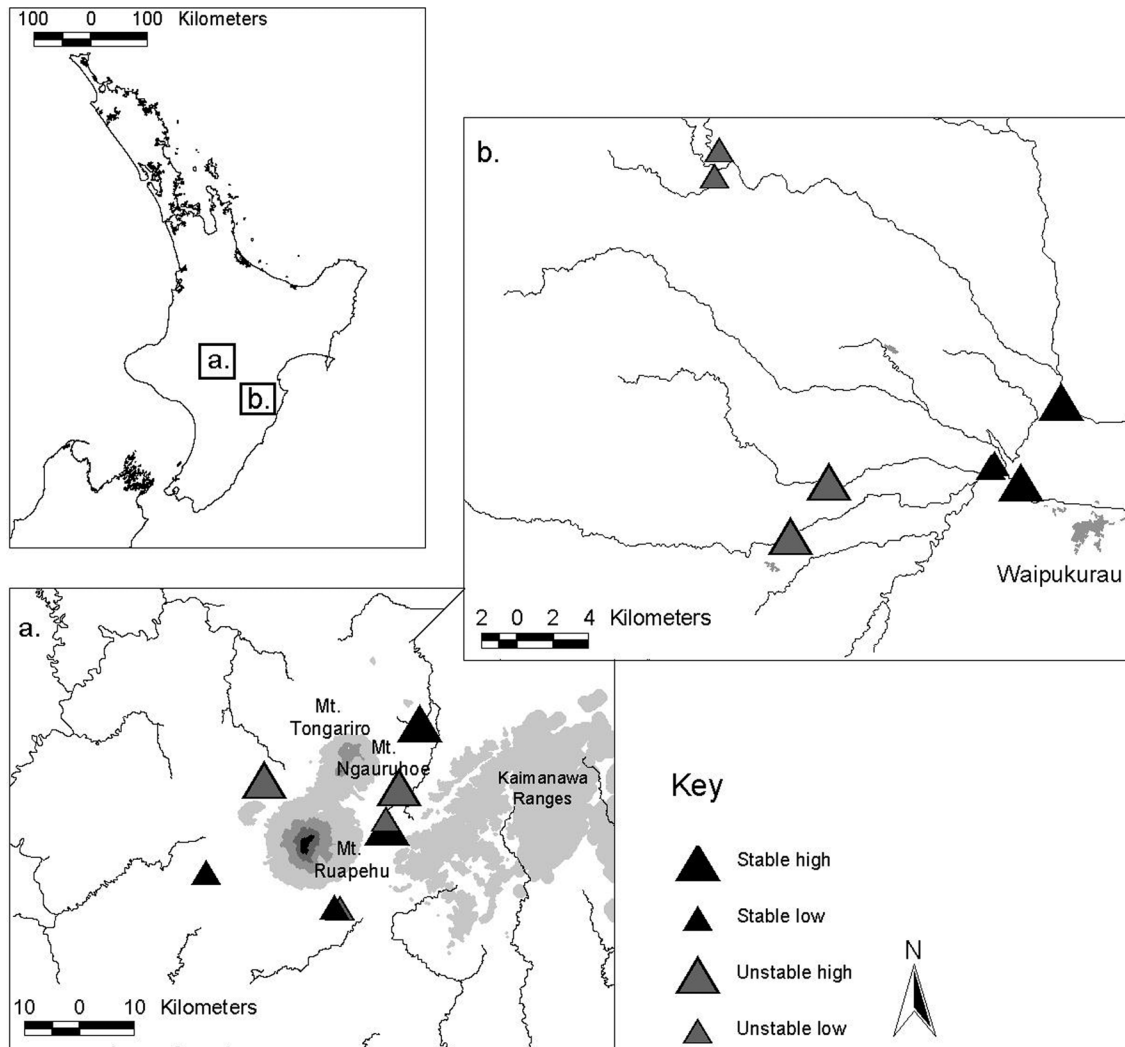


Fig. A1. Map showing location of the 16 study sites in two regions of the North Island of New Zealand collected on four occasions between February 2008 and July 2009. (a) Tongariro National Park (pristine) and (b) Hawke's Bay (non-pristine). The key shows the difference between stable and unstable and low and high productivity sites based on a priori selection. Note some sampling sites are hidden due to their close proximity to other sites.

## APPENDIX B

Table B1. Mean physicochemical characteristics and a priori selected stability and productivity groups for the 16 study streams collected on four occasions between February 2008 and July 2009 in the North Island of New Zealand.

Site	Location	Alt. (m)	Width (m)	Depth (cm)	Vel†	Cond.‡	Temp. (°C)	Moved	Stab.	Prod.
HB1	Makaroro River @ Maka. Rd	312	5.7	17.0	0.30	93.3	12.7	95.0	U	Low
HB2	Waipawa River @ Waka. Rd	315	6.7	19.4	0.48	96.7	12.8	76.7	U	Low
HB3	Spring creek @ Swamp Rd	146	4.7	43.6	1.52	170.0	13.7	3.3	S	High
HB4	Spring creek @ Lyndsay Rd	134	3.8	22.0	1.17	230.0	14.6	40.0	S	High
HB5	Makaretu Riv. @ Burnside Rd	216	5.3	15.8	0.87	96.7	12.9	60.0	U	High
HB6	Tukipo Riv. @ Burnside Rd	191	7.0	15.0	0.20	150.0	15.0	30.0	U	High
HB7	Spring 1 @ Onga. Waipuk. Rd	143	1.5	15.2	0.42	153.3	14.8	13.3	S	Low
HB8	Spring 2 @ Onga. Waipuk. Rd	139	3.2	75.6	0.07	110.0	15.5	0.0	S	Low
NP1	Wahianoa stream u/s intake	934	6.1	25.6	0.97	70.0	9.4	50.0	U	Low
NP2	Unnamed Karioi forest stream	935	3.5	22.6	0.96	139.7	8.6	30.0	S	Low
NP3	Orautoha stream @ middle Rd	712	2.5	24.4	0.55	92.7	8.2	8.3	S	Low
NP4	Whakapapaiti @ SH4	859	15.8	28.2	0.98	106.0	8.1	28.3	U	High
NP5	Te Piripi stream @ SH1	993	2.2	16.6	0.67	67.7	9.1	10.0	S	High
NP6	Mangatoetoenui @ SH1	971	9.4	44.2	0.96	133.0	9.5	25.0	U	Low
NP7	Oturere Stream SH1	809	9.4	42.4	0.86	110.7	8.6	8.3	U	High
NP8	Poutu Stream	518	7.7	43.6	1.05	70.3	8.9	8.3	S	High

Notes: HB = Hawke's Bay (non-pristine), NP = Tongariro (pristine), Alt. = altitude, Vel. = velocity, Cond. = conductivity, Temp. = temperature, Moved = % stone movement, Stab. = stability, Prod. = productivity, U = unstable, S = stable.

† Units =  $\text{m s}^{-1}$ .

‡ Units =  $\mu\text{S cm}^{-1}$ .

## APPENDIX C

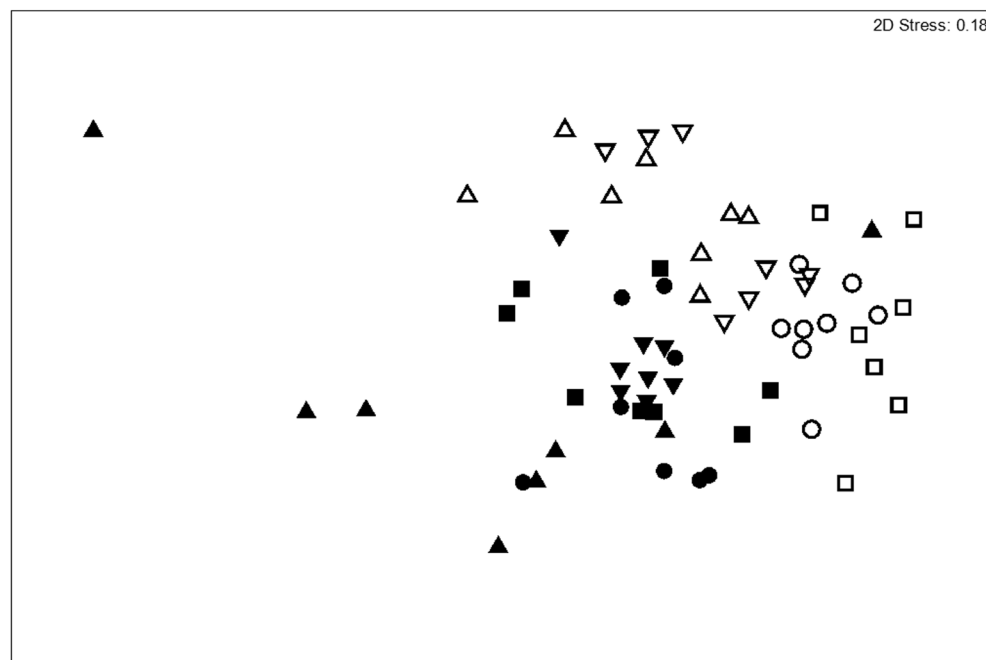


Fig. C1. Non-metric multidimensional scaling (NMDS) ordination on  $\log(x + 1)$  transformed data for 16 streams collected on four occasions between February 2008 and July 2009 in the North Island of New Zealand. Closed symbols are pristine sites (Tongariro Region), open symbols are non-pristine sites (Hawke's Bay region). Unstable/low productivity: upright triangles; Unstable/high productivity: inverted triangles; Stable/low productivity: squares; Stable/high productivity: circles.

## APPENDIX D

Table D1. Model coefficients results for five models predicting mean number of taxa collected from 16 North Island, New Zealand sites on four occasions between February 2008 and July 2009 with all sites included, pristine only (Tongariro) and non-pristine only (Hawke's Bay) sites.

Source	All sites		Pristine		Non-pristine	
	Coefficient (SE)	<i>t</i>	Coefficient (SE)	<i>t</i>	Coefficient (SE)	<i>t</i>
DEM						
y0	1.07 (0.06)	18.14***	1.03 (0.08)	13.13***	1.11 (0.08)	13.28***
D	0.004 (0.003)	1.55	0.01 (0.006)	1.75	0.004 (0.003)	1.49
P	0.79 (0.28)	2.82**	1.06 (0.42)	2.54*	0.65 (0.36)	1.79
D <sup>2</sup>	-0.00006 (0.00002)	-2.44*	-0.0001 (0.00001)	-2.38*	-0.0001 (0.00002)	-2.4*
P <sup>2</sup>	0.6 (0.28)	-2.17*	-0.76 (0.4)	-1.91	-0.65 (0.38)	-1.73
D × P	0.0001 (0.005)	0.02	-0.03 (0.02)	-1.02	-0.0004 (0.004)	-0.12
Death						
y0	1.36 (0.04)	37.99***	1.41 (0.07)	20.63***	1.31 (0.03)	46.71***
D	-0.001 (0.0006)	-2.01*	-0.002 (0.001)	-1.46	-0.002 (0.001)	-2.87**
P	0.07 (0.02)	3.83***	0.1 (0.04)	2.7*	0.04 (0.02)	2.36*
Death (with interaction)						
y0	1.36 (0.05)	29.78***	1.38 (0.08)	17.91***	1.3 (0.04)	30.93***
D	-0.001 (0.0009)	-1.31	-0.003 (0.002)	-1.55	-0.002 (0.001)	-1.78
P	0.08 (0.03)	2.92**	0.09 (0.04)	2.25*	0.03 (0.03)	1.13
D × P	-0.0003 (0.005)	-0.06	0.01 (0.02)	0.62	0.001 (0.004)	0.3
Tonkin						
y0	1.34 (0.04)	36.88***	1.37 (0.07)	19.9***	1.25 (0.03)	40.64***
D	0.004 (0.002)	1.56	0.005 (0.004)	1.27	0.002 (0.03)	0.98
P	0.07 (0.02)	3.86***	0.09 (0.04)	2.49**	-0.002 (0.07)	-0.02
D <sup>2</sup>	-0.00005 (0.00002)	-2.21*	-0.0001 (0.00004)	-1.92	-0.00004 (0.00002)	-2.13*
Tonkin (with interaction)						
y0	1.36 (0.04)	30.8***	1.39 (0.07)	19.07***	1.32 (0.04)	34.31***
D	0.005 (0.003)	1.76	0.01 (0.01)	1.63	0.01 (0.003)	1.92
P	0.09 (0.03)	3.43**	0.1 (0.04)	2.72*	0.07 (0.03)	2.31*
D <sup>2</sup>	-0.00006 (0.00002)	-2.36*	-0.0001 (0.0001)	-2.11*	-0.0001 (0.00002)	-2.68*
D × P	-0.005 (0.005)	-0.84	-0.03 (0.03)	-1.08	-0.005 (0.005)	-1.08

Notes: With interaction indicates the productivity × disturbance interaction term is included in the model. D = disturbance and P = productivity.

\**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001.