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The effects of productivity and disturbance on diversity in stream communities

A thesis presented in partial fulfilment of the requirements for the degree of

Doctor of Philosophy

in Ecology

at

Massey University, Palmerston North, New Zealand.

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2010

Abstract

The application of conventional diversity models in streams has had limited success as stream communities often fit outside the model assumptions. Of the plethora of influences on stream macroinvertebrate diversity, productivity and disturbance dominate. Yet there remains to be a consensus on the form of these relationships and whether productivity and disturbance interact to predict diversity. Therefore, the aim of this thesis was to assess linkages between productivity, disturbance and diversity in stream macroinvertebrate communities and further the understanding of these links. I achieved this through multiple assessments throughout New Zealand (NZ) and Spain between February 2007 and December 2009. I (i) assessed multivariate models of productivity-disturbance-diversity within NZ streams and examined whether canopy presence modulated these links and (ii) whether land-use affected these relationships. I further assessed (iii) the productivity-diversity relationship in Spanish streams and whether this was underpinned by specific periphyton-invertebrate associations and (iv) if the relationship matched those of NZ and formed a global trend. Finally, I experimentally examined (v) the influence of spatial scale on productivity- and disturbance-diversity relationships. The prevailing premise throughout the thesis is that diversity increased with increasing productivity and declined with increasing disturbance, although the form of these links varied. There was no evidence of a productivity-disturbance interaction throughout this thesis and these relationships were not affected by land-use but were by canopy presence. Where relationships with productivity lacked, I demonstrate this link may be underpinned by interactions between invertebrates and specific forms of algae, as well as simply being a function of the range of productivity assessed or even the spatial scale of assessment. In fact, productivity setting the upper limit to richness may be a universal pattern in streams with no evidence of productivity leading to greater competitive interactions despite the wide ranges assessed. Overall, this thesis makes significant progress in clarifying these relationships in streams. I provide further evidence suggesting the DEM does not apply in stream communities and clearly demonstrate additive, rather than interactive, effects of productivity and disturbance.

*To my parents
Roger and Jane Tonkin
who have given me the strength to undertake such a monumental task
and provided never-ending support.
Thank you.*

Acknowledgements

Firstly, I must thank my chief supervisor Associate Professor Russell Death for his guidance over the past four years. Russell has played a large part in my development as a scientist. From day one, he encouraged independent thought and taught me to stand alone as a scientist. Russell has shown great patience as a supervisor through times of lack of motivation or even over-excitement at times. For your help and guidance I am deeply grateful.

Thank you to my two co-supervisors Dr Mike Joy and Dr Kevin Collier, who I knew I could rely on for help and advice throughout my PhD. I may not have used your expertise to the fullest but when you were called on the assistance was extremely valuable, especially in the planning stages of the PhD and all the questions along the way. I am grateful for the support of Dr Jose Barquin during my trip to Spain and for arranging much of the logistical side of the research I carried out there.

Thanks to the Ecology Group staff including Fiona Death, Barbara Just, Erica Dahya, Tracey Harris, and Paul Barrett for all the logistical support. Special thanks must go to Cleland Wallace who on several occasions had to help sort supplies or make things for me at the last minute. I would like to acknowledge the financial support of a Massey University Doctoral Scholarship during my study for which I am grateful.

I am grateful to Keith Wood at Ernslaw One Limited for providing logistical support and access to Karioi Forest sites. Dr Michel Dedual and Glenn Mclean of the Department of Conservation, Turangi provided logistical support during the early stages of the thesis. Dr Mike Scarsbrook provided information on spring locations throughout the North Island. Dr Barry Biggs of NIWA provided useful help with regard to the design of Chapter 2. Jarrod Bowler and Bonny Lawrence at Genesis energy provided information on the location of dams within the Tongariro region.

To all my fieldwork assistants: Manas Chakraborty, Logan Brown, Esta Chappell, Nicki Atkinson, Amber McEwan, Jess Costall, Roger Tonkin, Brendon Fry, Alana Lawrence, Charlie Charles, Amy MacDonald, Ketan Parsot – thank you so much! Without your help, the work wouldn't have been possible. Special thanks goes to Brendon Fry for the long days of field work in order to get some fly fishing in. Thanks to Alana Lawrence and Travis Delich for all the free accommodation provided during

field work. Dr Richard Seaton deserves mention for his guidance from a perspective of someone who had 'been there and done that'. Thanks also to Ecology Group post graduate students for useful discussions on all things ecology, particularly Arved Schwendel who shared supervisor and subject.

I don't know where to begin to thank my family. Mum, Dad, Dan and Ami, the never-ending and unquestionable support you've given me over the past few years is nothing short of amazing! There's not much else I can say other than I will be forever grateful and I hope this thesis goes some way towards repaying all the effort you've put in!

Finally, no end of thanks will ever do justice to the amount of support my partner, Esta Chappell, has given me. I'm not sure how you dealt with my daily panic attacks and mood swings so well, you have the patience of a saint. You've sacrificed your weekends and social life for far too long. I for sure would have gotten rid of me by this stage. Thank you.

Thesis structure and authorship

This PhD thesis is a combination of five individual papers written as manuscripts for publication in refereed journals, in addition to the general introduction and synthesis. This has led to unavoidable repetition in some of the content between the five chapters, especially in the methods sections. Also, the numbers for all figures and tables restart for each chapter. Papers are co-authored in order to acknowledge significant contribution towards the paper including input into the original thesis concept, designing the research, administration, and editing manuscripts. Chapter 2 “Do productivity and disturbance interact to modulate macroinvertebrate diversity in streams?” has been submitted to *Oikos* and is co-authored by Russell Death and Kevin Collier. Chapter 3 “Consistent effects of productivity and disturbance on diversity between landscapes” has been submitted to *Ecology* and is co-authored by Russell Death. Chapter 4 “Productivity-diversity relationships in streams and the role of periphyton assemblages” has not been submitted to any journal but will be co-authored by Russell Death and Jose Barquin, as will Chapter 5 “Global patterns in stream diversity – productivity relationships”. Chapter 6 “Scale dependent effects of productivity and disturbance on diversity” has not been submitted for publication but will be co-authored by Russell Death. For all chapters in this thesis, my input was the greatest. I planned the research, carried out the field and lab work, analysed all of the data and wrote all of the content.

Signed by all involved co-authors:

Russell Death



Kevin Collier



Jose Barquin



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Chapter 1

General Introduction



Establishing what affects diversity in nature remains a central theme in ecology (Huston 1994, Rosenzweig 1995, Hubbell 2001). Although diversity can be affected by a variety of factors (e.g. temperature, disturbance, productivity, habitat complexity), there is still considerable debate about how they might interact (Huston 1994, Palmer 1994, Rosenzweig 1995, Vinson and Hawkins 1998, Hubbell 2001, Ricklefs 2004). Moreover, although increasing application of multivariate models suggests ecologists recognise that univariate examinations are limited (Wootton 1998, Mackey and Currie 2001, Roxburgh et al. 2004, Cardinale et al. 2006), there remains considerable uncertainty as to which factors explain the majority of variation in diversity (Mackey and Currie 2001). However, disturbance (Connell 1978, Wootton 1998, Lake 2000) and productivity (Currie 1991, Waide et al. 1999, Mittelbach et al. 2001) continue to dominate the research interests of community ecologists although universal patterns of diversity remain elusive (Waide et al. 1999, Mackey and Currie 2001, Mittelbach et al. 2001). In fact, evidence suggests that disturbance and productivity interact to affect diversity (Sousa 1984, Pickett and White 1985, Currie 1991, Wootton 1998, Waide et al. 1999, Mittelbach et al. 2001, Death and Zimmermann 2005, Cardinale et al. 2006).

There have been many attempts to define disturbance such as that put forward by Pickett and White (1985) where they suggest disturbance is "... any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment". However, it is tautological to define disturbance by the effects on biota rather than the physical act of disturbance itself, especially with stream invertebrate communities where animals are 'adapted' to these events (Resh et al. 1988, Lake 2000, Death 2010). Thus, using the definitions put forward by Bender et al. (1984) and Glasby and Underwood (1996), Lake (2000) suggests disturbance is "the cause of a perturbation", where perturbations are a combination of cause (disturbance) and effect (response to disturbance).

Two of the most longstanding models of diversity are the Intermediate Disturbance Hypothesis (IDH) (Grime 1973b, Connell 1978, Sousa 1979) and the Dynamic Equilibrium Model (DEM) (Huston 1979, 1994). The IDH predicts diversity to

peak at intermediate levels of disturbance, and the DEM builds on this to predict the position of the peak of diversity to vary with productivity. Models such as the IDH and the DEM assume a trade-off between competitive and colonisation ability whereby organisms are either good colonisers or good competitors, but not both (Chesson and Huntly 1997, Roxburgh et al. 2004, Cadotte 2007). However, this does not appear to occur in many ecosystems and has led some to suggest disturbance simply removes taxa (e.g. Death and Winterbourn 1995, Death 2002) as opposed to promoting diversity at intermediate levels by allowing the representation of the largest number of life-history traits. Moreover, the disturbance-diversity relationship is highly variable between unimodal, positive linear and negative linear forms, or even no relationship (Mackey and Currie 2001), and can vary with spatial and temporal scale (Petraitis et al. 1989). Mackey and Currie (2000) found little evidence to suggest that disturbance should play more than a minor role in determining diversity patterns.

The relationship between productivity and diversity is also highly variable (Currie 1991, Abrams 1995, Waide et al. 1999, Mittelbach et al. 2001). The most common forms are unimodal (e.g. Grime 1973a, Huston 1979, Rosenzweig 1992, 1995, Leibold 1999, Waide et al. 1999, Mittelbach et al. 2001) or linear (e.g. Currie and Paquin 1987, Currie 1991, Abrams 1995, Waide et al. 1999, Gaston 2000, Mittelbach et al. 2001) increases in diversity with increasing productivity. The spatial scale of observation is one of the major reasons for the differences in the nature of this relationship such as the switch from unimodal to linear as scale increases (Currie 1991, Chase and Leibold 2002), but it also differs between ecosystems and organisms (Waide et al. 1999, Mittelbach et al. 2001). Small scale studies commonly find unimodal relationships between productivity and diversity but at greater spatial scales the pattern is one of monotonic increase in diversity with productivity (Waide et al. 1999, Mittelbach et al. 2001, Chase and Leibold 2002). The most commonly postulated mechanism for the decline in diversity at high productivity is competitive exclusion (Rosenzweig and Abramsky 1993, Abrams 1995, Waide et al. 1999); although Abrams (1995) provides several alternative reasons for this pattern such as larger individuals at higher productivities and the fact high productivity environments often occur at the extremes of geographical gradients.

Streams and rivers are heavily influenced by disturbance (Resh et al. 1988, Lake 2000, Death 2008), but the response of diversity to disturbance is likely to be dependent on productivity (Death 2002, Cardinale et al. 2005, Death and Zimmermann 2005, Cardinale et al. 2006). Several empirical studies have found an interaction between productivity and disturbance to be important in controlling diversity (e.g. Wilson and Tilman 2002, Kneitel and Chase 2004, Death and Zimmermann 2005, Scholes et al. 2005). In fact, the DEM infers richness is a product of productivity, disturbance and their interaction (Huston 1979, 1994, Kondoh 2001). However, the highly mobile nature of stream invertebrates has limited the applicability of common models of diversity such as the IDH (Grime 1973b, Connell 1978, Sousa 1979) and the DEM (Huston 1979, 1994, Kondoh 2001), but see Townsend et al. (1997). Streams have an especially strong association between disturbance and productivity, and disturbance acts by removing both taxa and their food resources (Lake 2000, Death 2002, Death 2010).

The requirement for a trade-off in competitive and colonising ability in these models (Chesson and Huntly 1997, Roxburgh et al. 2004, Cadotte 2007) and the fact that there appears to be little evidence for the generality of competitive exclusion in stream communities (Reice 1985, Death and Winterbourn 1995), indicates it is more likely that the number of animals and/or taxa is determined by the productivity/resource supply rates of a site (Death 2002, Gross and Cardinale 2007, Death 2008). Nonetheless, there is certainly strong evidence for competitive interactions and indeed competitive exclusion in streams (McAuliffe 1984, Kohler 1992), none more evident than Kohler and Wiley's (1997) investigation of pathogen outbreaks in Michigan streams. However, it appears physical processes are often dominant over biotic interactions in streams, especially in New Zealand (Thompson and Townsend 2000). This modulation of competition by abiotic and indeed biotic processes is well recognised for streams worldwide making the clarification of its effects a challenge (Holomuzki et al. 2010). An example of this is the strengthening of predation and competition during low-flow disturbance events (Dewson et al. 2007).

Accordingly, it is important for benthic ecologists to develop and apply models relevant to the type of communities present in streams. Death (2002) proposed a

model suggesting disturbance simply resets the colonisation process of invertebrates; and productivity, rather than competitive interactions, sets the upper limit to richness in streams. Yet, there is little consensus on quite how diversity responds to productivity and disturbance in streams. In fact, little effort has been placed on clearly defining the relationship between productivity and diversity in lotic systems. Some of the few to look specifically have found both unimodal (Death and Zimmermann 2005) and log-linear (Death 2002, Barquin 2004) increases in diversity with increasing productivity. Streams provide a unique testing ground for productivity-disturbance-diversity models because community dynamics are dominated by immigration and emigration rather than population growth (Downes 1990, Death 2008). The major models should not apply in lotic communities which are dominated by highly mobile taxa rather than sedentary organisms such as plants and corals for which many of these models have been developed.

Primary productivity is typically provided in streams by periphytic algae which can vary strongly in form from prostrate and stalked diatoms through to filamentous green algae (Allan 1995). The measurement of primary productivity does not account for variation in the form of these producers which can respond differently to environmental conditions and provide different habitat and resources for higher trophic levels. When levels of periphyton reach greater densities and epilithic diatoms are replaced by macroalgae such as filamentous green algae, interactions can shift from simple plant-herbivore interactions to more complex relationships where macroalgae can both provide and remove habitat and food, and compete for space with certain invertebrate taxa (Dudley et al. 1986). One example of this is the typical transition from pollution sensitive invertebrate taxa associated with diatom communities to pollution tolerant taxa and filamentous algae growth forms often found in summer low-flow conditions (Suren et al. 2003). Finally, although grazing control of periphyton is strong in lotic systems (Hillebrand 2009), this can differ between different growth forms (Feminella and Hawkins 1995). For example, where diatom levels remain relatively stable at low biomass with strong top-down control, filamentous forms can escape grazing and dominate (Suren and Riis 2010). However, this may only be an initial response before grazers respond and regulate biomass

(Lamberti et al. 1989). Thus, assessing the response of higher trophic levels to periphyton forms is likely to be complicated by this differential top-down control by grazers through time and may be a reason for prior research of this relationship being heavily focused on top-down, rather than bottom-up, control.

Measurement of both gross primary productivity (GPP) and net primary productivity (NPP) in streams has proven troublesome for lotic ecologists compared to other systems (Allan 1995). There are however, several approaches to doing so, all with issues in their reliability including biomass accrual over time and stream gas exchange (O_2 or CO_2) (Allan 1995), although novel approaches have been taken in streams in recent years (Hill and Dimick 2002, Hill et al. 2010). Often these approaches are less than satisfactory for stream ecosystems with low productivity levels due to several factors such as the requirement of estimating diffusion between water and air, and the inability to limit these measurements to stream autotrophs. Due to the difficulties in measuring primary productivity in nature, especially in well spatially or temporally replicated studies, surrogates are widely used such as biomass, precipitation, actual evapotranspiration (AET), potential evapotranspiration (PET), and soil nutrient status (Waide et al. 1999, Mittelbach et al. 2001, Gillman and Wright 2006). Inconsistent use of these proxies and nonlinear trends with actual primary productivity has stymied attempts at deciphering patterns (Whittaker 2010).

Standing crop of periphyton biomass is commonly used as a surrogate for primary productivity in streams (Morin et al. 1999). Morin et al. (1999) reviewed the relationship between standing crop chlorophyll *a* and primary productivity in streams over a large range of both metrics spanning four orders of magnitude and found a strong link between the two ($r^2 = 0.63$). They suggest this surrogate would be useful as a coarse estimate of production, but also advocate the addition of temperature as a covariate. However, it has been recognised that maximum biomass can be a poor surrogate where herbivory is severe (McNaughton 1985). Another inherent problem with this relationship is the decline in primary productivity with increased chlorophyll *a* standing stock (Morin et al. 1999 and references therein). There are multiple mechanisms that may lead to this including self shading and shifts in composition of periphyton (Dudley et al. 1986, Morin et al. 1999).

It is also important to consider that primary productivity is not the sole food base of stream communities. Allocthonous detrital input is the other major food base component of these ecosystems (Minshall 1967, Tank et al. 2010, Finlay 2011). In fact, early research suggested streams were heterotrophic in nature, depending heavily on detritus inputs (Tank et al. 2010 and references therein), however recent work in tropical headwater streams may suggest the opposite (Lau et al. 2009). In New Zealand, streams often have a large proportion of their length unshaded and thus are dominated by primary production (Thompson and Townsend 2000) and low proportions of shredders (Winterbourn et al. 1981, Winterbourn 1997). While both heterotrophic and autotrophic production are deemed to be highly important to stream communities, I have chosen to focus on algal based community production in this thesis and accept the caveats with the use of standing crop of periphyton biomass as a surrogate of primary productivity.

There is a plethora of other factors that can influence stream communities (Vinson and Hawkins 1998). However, changes in land use such as agricultural intensification can severely alter communities living within these landscapes (Harding et al. 1998, Allan 2004, Tschardt et al. 2005) and are impacting negatively on habitats worldwide (Tilman 1999, Allan 2004, Foley et al. 2005). Changes in land use can both alter the composition of stream communities and cause changes in the flood regime (Rowe et al. 1997, Walsh et al. 2005). Pastoral development in particular can impact on stream communities through a suite of mechanisms such as changes to hydrology, sediment regimes, channel morphology and temperature (Quinn 2000, Allan 2004). However, the effects of agricultural intensification on flood influences is relatively unknown (Death 2008). One influence thought to strongly impact stream communities which can occur through land use change is the presence or absence of canopy cover. In small streams this can influence the way in which disturbance affects macroinvertebrate diversity by altering primary productivity patterns (Robinson and Minshall 1986, Death 2002, Death and Zimmermann 2005, Fuller et al. 2008). Due to their strong colonising abilities (Mackay 1992, Allan 1995), post-flood recovery of the food base in autotrophic streams is likely the major determinant of invertebrate diversity; however this may not apply in heterotrophic streams if the resource base is

relatively unaffected by disturbance (Death and Zimmermann 2005, Fuller et al. 2008). This contrasting response of lotic invertebrates between autotrophic and heterotrophic streams is likely to hinder the generalised application of models such as the DEM.

It is clear that diversity can be affected by countless environmental influences (Rosenzweig 1995). However, as with inconsistent environmental sampling, lack of reliable diversity measures has likely hindered progress towards resolution of such relationships. Diversity can be coarsely broken down into two main aspects – richness and evenness, and many indices attempt to merge these (Magurran 2004). In fact many people, including myself throughout this thesis, interchange the terms richness and diversity (Magurran 2004). There is still little consensus on which measure is best as many can obscure patterns, hence the ongoing development of diversity indices including measures of taxonomic distinctness (Clarke and Warwick 1998). What is more, these indices assess diversity at its lowest resolution and do not account for different scales of diversity including β -diversity which has received significant attention in recent years (e.g. Chase and Leibold 2002, Chase 2010). Moreover, there is also the question as to whether the number of taxa per unit of area or per unit of animals collected, which can be accounted for using rarefaction (Hurlbert 1971), is more important. The approach I take throughout this thesis is to assess whether richness, namely the number of taxa per unit area, responds to both productivity and disturbance. Where other indices have been used it is specific to each chapter. I take an approach that minimises haphazard selection of multiple indices that is common among researchers in order to find the best patterns on an *ad hoc* basis (Magurran 2004). It is important to note here that these indices are considered supplementary to the simple richness measure which forms the basis of this thesis.

A note on statistical paradigms used throughout the thesis

Model selection is a troublesome concept in ecology. Historically, ecologists have focused almost entirely on classical statistics revolving around the hypothetico-deductive approach with the ever abundant (if not overused) p-value. However, this is complicated by the fact that ecological data often does not fit the assumptions of

classical statistics through issues such as lack of replication, unequal variances and unbalanced designs. Burnham and Anderson (2002) advocate a departure from this with the information-theoretic approach focusing heavily on model selection using Akaike's information criterion (AIC) (Akaike 1974) rather than falsifying hypotheses. It is important to note that AIC does not represent a 'true' model, but merely indicates the 'best' model of those selected. Thus, I take a mix of approaches throughout this thesis incorporating mostly classical hypothesis testing but when assessing the fit of multiple models I adopt an information-theoretic approach to model selection.

Thesis structure and aims

These uncertainties in relationships between diversity, disturbance and productivity, especially in streams, led me to this study to examine the linkages between productivity, disturbance and diversity of macroinvertebrate communities in streams. The objectives of each of the remaining six chapters are as follows:

- **Chapter 2** examines the relationship between productivity, disturbance and diversity in mountain streams in the central North Island of New Zealand. This chapter assesses the application of the DEM in these stream communities and I develop a new model for the prediction of taxonomic richness by productivity and disturbance in streams. Moreover, I assess whether the presence of canopy cover confounds the relationship between productivity, disturbance and diversity in streams.
- **Chapter 3** investigates whether the relationship between productivity, disturbance and diversity is consistent between landscapes. Due to the level of land use change worldwide it is important to consider whether it can affect these relationships. Thus, I test whether the productivity-disturbance-diversity relationship differs between a pristine region (Tongariro National Park) and a more altered region (central Hawke's Bay) through land clearance and pastoral farming. The streams in this chapter were sampled multiple times to evaluate seasonal variation and, to test the productivity-disturbance-diversity relationship, I fit these data to the DEM, the model developed in Chapter 2, and Death's (2002) model of diversity.

- **Chapter 4** assesses the relationship between productivity and diversity in streams of Cantabria in northern Spain. Lack of direct assessment of the productivity-diversity relationship in streams outside of New Zealand led me to assess the link in Spanish streams in order to provide more in depth analysis of this relationship. I assess whether there is a clear relationship between productivity and diversity in these streams, or whether underlying biological interactions between invertebrates and periphyton are more important. That is, I test whether underlying relationships between invertebrates and the main growth forms of periphyton are better at predicting community metrics in stream than a simple productivity measure.
- **Chapter 5** examines whether there is a consistent productivity-diversity relationship in lotic systems at two locations around the world. For this I compare the productivity-diversity relationship between streams of the central North Island of New Zealand and those of northern Spain. I further explore this relationship to assess whether differences in patterns are simply due to measurement along different environmental scales and assess whether combining these regions can yield a universal productivity-diversity relationship for streams.
- **Chapter 6** uses experimental channels in spring-fed streams in order to assess both productivity- and disturbance-diversity relationships and whether these differ with the scale of observation. Specifically, I use proxies of large scale patterns such as α , β and γ diversity by assessing taxonomic richness at within- and between-stream scales, and between-stream community dissimilarity; and I examine whether the form of these relationships differ between scales using experimental levels of productivity and disturbance. I discuss possible causes for differences between scales such as community assembly rules.
- **Chapter 7** briefly synthesises the findings throughout the five main chapters of this thesis.

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Chapter 2

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



Abstract

The application of diversity models in lotic systems has been somewhat unsuccessful as stream communities don't often fit conventional model assumptions. Although it is clear that disturbance and productivity are dominant forces in lotic systems, the inability of the Dynamic Equilibrium Model (DEM) to explain observed patterns suggests specific models are required for these systems that are not constrained by competitive-colonising trade-offs. We set out to (i) test the application of the DEM in 47 mountain streams in the central North Island of New Zealand and (ii) develop a modified model based on observed relationships in this study that accounts for the confounding influence of canopy cover. Although canopy cover had no influence on productivity, a link between disturbance and productivity was only found in open canopy streams where taxonomic richness increased log-linearly with increasing productivity and peaked at intermediate levels of disturbance. When accounting for evenness of communities, the results were more inconsistent exhibiting a decline with disturbance, but not at open canopy sites. However, both taxonomic richness and Simpson's diversity index were higher in closed canopy streams. Overall, we show that richness of stream invertebrates in the present study is a product of both disturbance and productivity but not of their interactive effects. Although there was a peak in richness at intermediate rates of disturbance, our results do not support the DEM. We suggest the combined effects of productivity and disturbance are additive rather than multiplicative supporting other studies that suggest productivity simply sets the upper limit to richness in streams.

Introduction

Establishing what 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 (Palmer 1994, Vinson and Hawkins 1998), 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, but the form of this interaction varies (Sousa 1984, Pickett and White 1985, Currie 1991, Wootton 1998, Waide et al. 1999, Mittelbach et al. 2001, Death and Zimmermann 2005, Cardinale et al. 2006).

Disturbance is one of the major structuring forces in lotic systems (Resh et al. 1988, Lake 2000, Death 2010). A dominant paradigm in disturbance ecology, the Intermediate Disturbance Hypothesis (IDH), has been amongst the most widely applied ecological theories (Grime 1973b, Connell 1978, Sousa 1979). However, there has been little empirical support for this hypothesis in streams, possibly because many stream organisms are highly mobile (but see Townsend et al. 1997). In fact, the literature suggests that the disturbance-diversity relationship is highly variable in nature generally (Mackey and Currie 2001). What is more surprising is that many studies show no or weak effects of disturbance on diversity or community structure (Mackey and Currie 2000). In lotic systems, the disturbance-diversity relationship can be confounded by the fact that disturbance not only acts directly on benthic invertebrates but indirectly by the removal of food resources (Death 2002). Thus several authors have proposed that the nature of the disturbance-diversity relationship is controlled by habitat productivity altering population growth rates (Huston 1979, 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, Waide et al. 1999, Mittelbach et al. 2001). However, just as with the disturbance-diversity relationship, the form of the relationship can be quite variable (Abrams 1995, Waide et al. 1999, Mittelbach et al. 2001). The most commonly reported relationships are unimodal (e.g. Grime 1973a, Huston 1979, Rosenzweig 1992, 1995, Leibold 1999, Waide et al. 1999, Mittelbach et

al. 2001) or linear (e.g. Currie and Paquin 1987, Currie 1991, Abrams 1995, Waide et al. 1999, Gaston 2000, 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 and Leibold 2002). However, local scale studies often find unimodal relationships (Waide et al. 1999, Mittelbach et al. 2001, Chase and Leibold 2002) which are potentially explained by many mechanisms (Rosenzweig and Abramsky 1993, Abrams 1995, Waide et al. 1999) that often require some form of competitive trade-off.

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. Using the patch occupancy models of Hastings (1980) and Tilman (1994), Kondoh (2001) expanded this model 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 various life-history traits. However, like the DEM, it also predicts that diversity will peak at intermediate levels of productivity and disturbance with the position of the peak on one scale depending on the level of the other. Models such as the IDH, DEM and Kondoh's model assume a trade-off between competitive and colonisation ability whereby organisms are either good colonisers or good competitors but not both (Chesson and Huntly 1997, Roxburgh et al. 2004, Cadotte 2007). There appears to be little evidence for the generality of competitive exclusion in stream communities (Reice 1985, Death and Winterbourn 1995), and it appears more likely that carrying capacity may be determined by the productivity/resource supply rates of a site (Gross and Cardinale 2007, Death 2008). Accordingly, Death (2002) proposed that in the absence of disturbance, resource levels rather than competitive interactions set an upper limit to the richness of communities through colonisation, whilst disturbance resets the colonisation process by removing animals and thus taxa, and resetting resource levels.

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 and Minshall 1986, Death 2002, Death and Zimmermann 2005, Fuller et al. 2008). As a large proportion of lotic invertebrates have good colonising abilities after disturbance (Mackay 1992, Allan 1995), it is likely that post-flood recovery of the food base is the major determinant of invertebrate diversity in autotrophic streams (Death and Zimmermann 2005). 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). Fuller et al. (2008) suggest that when periphyton recovery is not limited by nutrients, open canopy sites are more resilient to disturbance than sites with canopy cover. Conversely, sites with canopy cover are more resistant because the invertebrate community recovery is not as dependent on periphyton re-growth post disturbance as in open canopy sites (Fuller et al. 2008). The contrasting response of lotic invertebrates to productivity and disturbance between autotrophic and heterotrophic streams is likely to hinder the generalised application of models such as the DEM. That is, where retention of organic matter in forested streams is sufficient, macroinvertebrate communities are likely to respond differently to disturbance than in autotrophic streams as they are less dependent on primary 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, Sugden et al. 2008). However, the results have been equivocal with the response of communities to productivity and disturbance varying inconsistently between ecosystems and little evidence of interactive effects (but see Cardinale et al. 2006). In this study we test the DEM on benthic invertebrate 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 exclusively 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, and that this relationship will be stronger at open canopy sites than at sites with canopy due to tighter coupling with algal food resources. We discuss whether diversity patterns in

these streams can be better explained by a modified productivity-disturbance-diversity model that is not constrained by the competitive-colonising trade-off inherent with the DEM.

Methods

Study sites

Forty seven first- to sixth-order streams and rivers were selected for sampling around the mountains of the Tongariro National Park, New Zealand (Fig. 1). 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-kakaramaea 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 yr⁻¹, with the south and east only receiving around 1,100 mm yr⁻¹ 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 m² 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 and Peters 1996, Winterbourn et al. 2000). Taxa that could not be taken to species level were identified to morphospecies. Density (individuals 0.1 m^{-2}), number of taxa and Simpson's diversity index ($1-\lambda'$) (Simpson 1949) were calculated to summarise different aspects of diversity. These metrics were the mean values calculated for the five individual samples at each site.

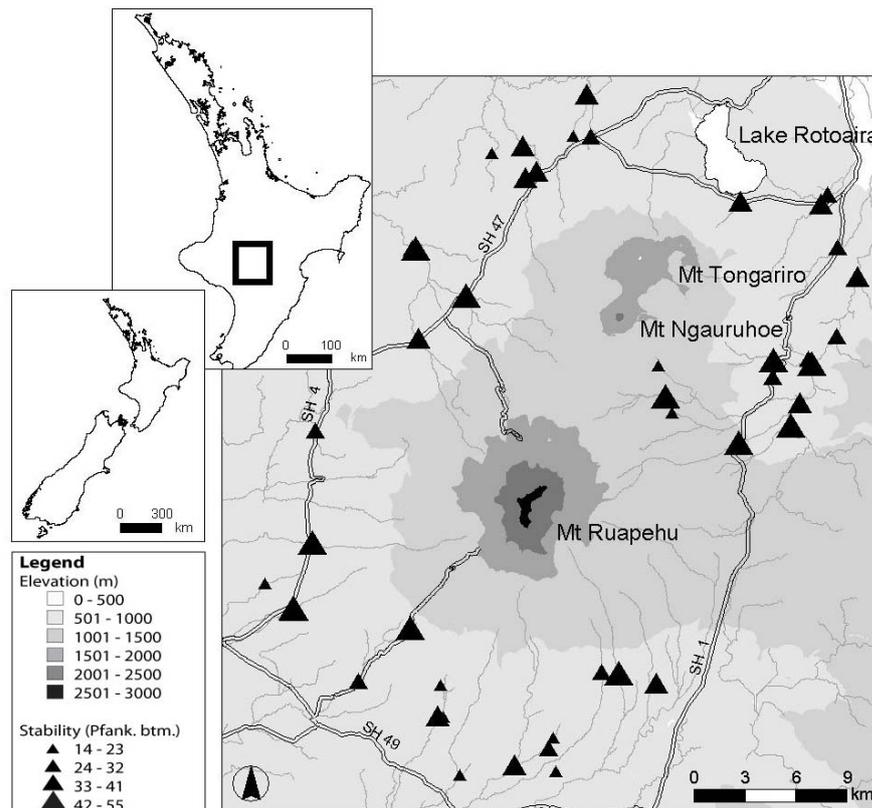


Figure 1: Location of 47 sites in the Tongariro National Park, central North Island, New Zealand, sampled between February and April 2007.

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 and Death (In prep.) found a strong link between biomass accumulation on artificial substrate 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^2) 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 Lamberti (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 and Collier 1987, Death and 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 (Quinn and Hickey 1990).

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. Fine particulate organic matter (FPOM) was not measured as POM has not been shown to be an important determinate of invertebrate community structure in New Zealand streams (Scrimgeour and Winterbourn 1989, Death and Winterbourn 1995). 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 divided in half 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, 17 of which had >50 % cover. 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 and Gorley 2006). We then used similarity percentages (SIMPER) (Clarke 1993) to explore which taxa contributed to the differences between canopy (Clarke and Gorley 2006).

In order to test for differences in physicochemical variables, 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, U.S.A.). 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 (Statistix 8 ©, Analytical Software, Tallahassee, FL, U.S.A.).

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:

$$S = b_0 + b_1P + b_2C + b_3P^2 + b_4C^2 + b_5PxC$$

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 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) ($F_{2,45} = 0.92$, $P = 0.41$). Spot temperature ranged from 6.6 to 17.6°C at all sites and was slightly lower in spring-fed streams ($F_{2,45} = 3.29$, $P = 0.047$) but did not differ with canopy cover (Table 1). Mean velocity and depth ranged from 0.16 to 1.46 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 was a strong structuring force acting 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* spp., the elm mid beetle larvae *Hydora* spp. and chironomid *Maoridiamesa* spp. were abundant at both open canopy and sites with canopy cover (>3.7 % contribution at both canopy treatments). 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 chironomids 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 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.

Table 1: Mean (\pm 1 S.E.) 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	<i>F</i> _{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 (m s ⁻¹)	0.89 (0.04)	0.67 (0.08)	6.53	0.014
Conductivity (μ S cm ⁻¹)	131.58 (14.15)	93.17 (7.66)	5.56	0.023
Temperature (°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
SI	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> (μ g cm ⁻²)	1.88 (0.3)	1.87 (0.23)	<0.01	0.98
No. of taxa 0.1 m ⁻²	14.78 (1.02)	18.02 (0.91)	5.6	0.022
No of individuals 0.1 m ⁻²	327.5 (59.52)	275.92 (32.15)	0.57	0.46
Simpson's (1 - λ')	0.74 (0.02)	0.81 (0.01)	9.52	0.004

Periphyton and stability

Chlorophyll *a* ranged from 0.03 to 5.02 μ g cm⁻² and averaged 1.87 μ g cm⁻². There was no difference in chlorophyll *a* between open and closed sites (Table 1), and providing

stream width as a covariate did not change this (ANCOVA: $F_{1,44} = 0.33$, $P = 0.57$). Sites with canopy cover were more stable (Pfankuch index) but differences in site stability did not account for the lack of difference in periphyton biomass between open canopy and sites with canopy cover (ANCOVA: $F_{1,44} = 0.14$, $P = 0.71$). Periphyton biomass was not related to stability (Pfankuch index) for all sites combined ($F_{1,45} = 1.21$, $P = 0.28$, $r^2 = 0.026$; Fig. 2) or for only sites with canopy cover ($F_{1,21} = 0.34$, $P = 0.57$, $r^2 = 0.02$; Fig. 2), but declined with decreasing stability at open sites ($F_{1,22} = 4.46$, $P = 0.05$, $r^2 = 0.17$; Fig. 2). In fact, multiple correlations show no single variable was related to periphyton biomass with all sites included. CPOM was not related to stability at all sites ($F_{1,45} = 0.46$, $P = 0.5$), open canopy sites ($F_{1,22} = 0.62$, $P = 0.44$) or sites with canopy cover ($F_{1,21} = 2.73$, $P = 0.11$).

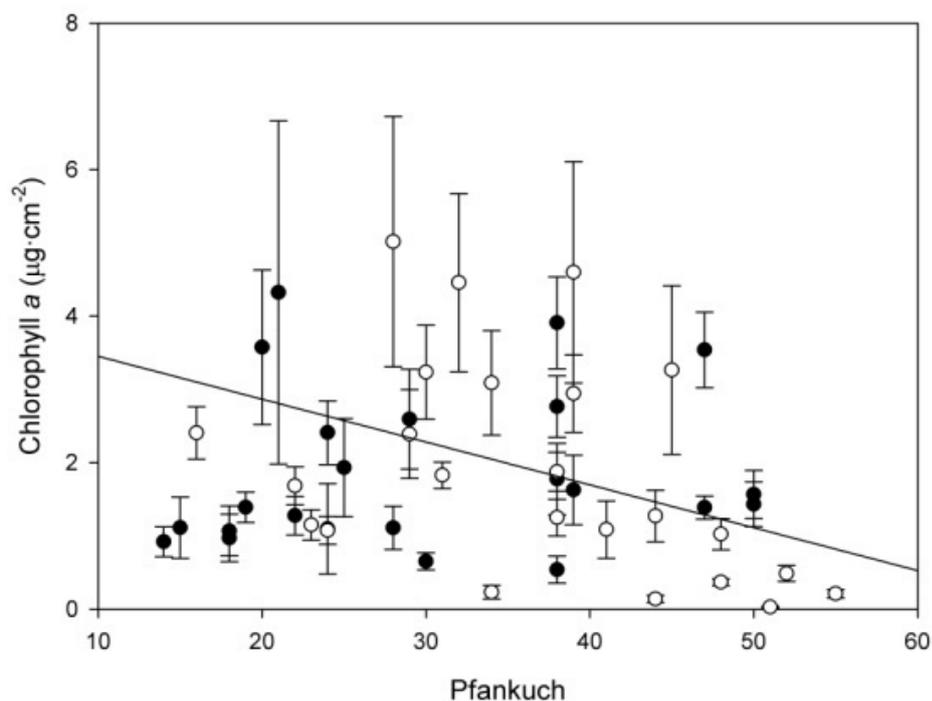


Figure 2: Mean (± 1 S.E.) chlorophyll *a* as a function of the bottom component of the Pfankuch stability index collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007. Open circles are open canopy streams and closed circles are sites with canopy cover. Regression line represents only open canopy sites; see text for fit statistics and equation.

Density and diversity

The mean total density of invertebrates in the benthos ranged from 3.8 individuals 0.1 m^{-2} at site 32 to 1205 individuals 0.1 m^{-2} at site 29. Density did not differ between

open canopy and sites with canopy cover (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. 3; Table 2) and peaked at low to intermediate levels of stability (Fig. 3; Table 2; AIC: -33.3) rather than declining monotonically ($F_{1,22} = 12.92$, $P = 0.001$, $r^2 = 0.37$; AIC: -32.4). No relationship with periphyton biomass or stability was evident at sites with canopy cover (Fig. 3; Table 2). The number of individuals was not related to CPOM at all sites ($F_{1,45} = 0.04$, $P = 0.84$), open sites ($F_{1,22} = 0.01$, $P = 0.94$) or sites with canopy cover ($F_{1,21} = 0.03$, $P = 0.87$).

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 Pfankuch 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. D.f. = degrees of freedom.

	D.f.	F	P	r^2	Equation
a) Pfankuch					
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) Chlorophyll a					
Density	1, 45	42.23	<0.0001	0.48	$y = 2.22 + 0.28 \cdot \ln(x)$
Open canopy	1, 22	36.07	<0.0001	0.62	$y = 2.24 + 0.31 \cdot \ln(x)$
Closed canopy	1, 21	2.99	0.099	0.13	Non-significant
No. of taxa	1, 45	25.54	<0.0001	0.36	$y = 15.48 + 2.97 \cdot \ln(x)$
Open canopy	1, 22	22.93	<0.0001	0.51	$y = 14.41 + 2.79 \cdot \ln(x)$
Closed canopy	1, 21	4.22	0.053	0.17	Non-significant

The mean number of taxa collected per sample averaged 16.4 taxa 0.1 m^{-2} ranging from 2.2 taxa 0.1 m^{-2} to 27.8 taxa 0.1 m^{-2} . Taxonomic richness was higher at sites with canopy cover than at open canopy sites (Table 1). Richness increased logarithmically with increasing periphyton biomass and peaked at intermediate levels of disturbance (Table 2). With open canopy sites considered separately, richness

increased logarithmically with increasing periphyton biomass and peaked at intermediate levels of disturbance (Fig. 4; Table 2). No relationship with periphyton biomass or stability was found at sites with canopy cover (Fig. 4; Table 2). The number of taxa was not related to CPOM at all sites ($F_{1,45} = 3.79, P = 0.058$), open sites ($F_{1,22} = 1.47, P = 0.24$) or sites with canopy cover ($F_{1,21} = 0.49, P = 0.49$).

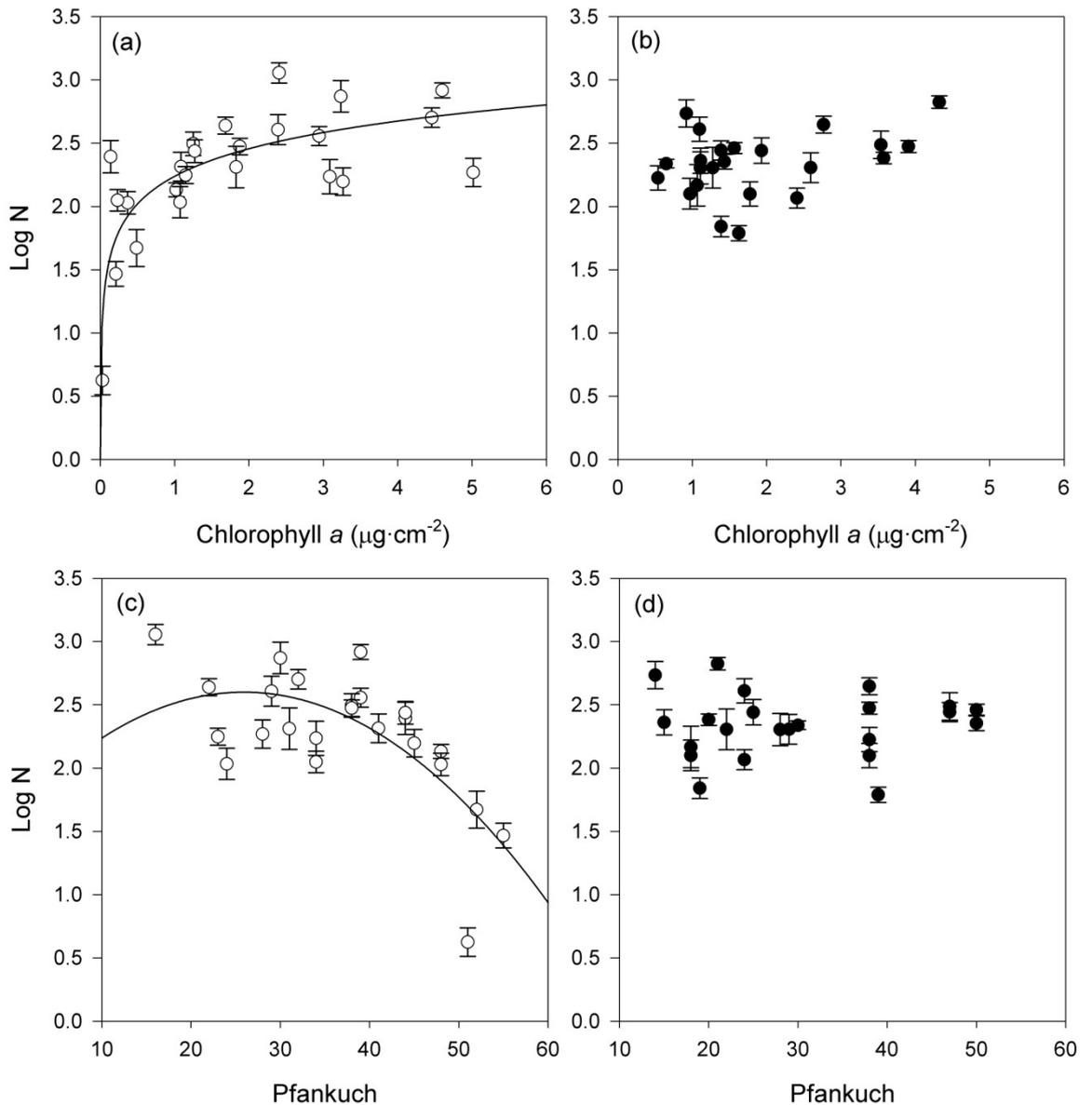


Figure 3: Mean (± 1 S.E.) log number of animals as a function of (a, b) chlorophyll *a* and (c, d) bottom component of Pfankuch stability index collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007. (a, c) Open canopy sites and (b, d) sites with canopy cover. See Table 2 for regression results.

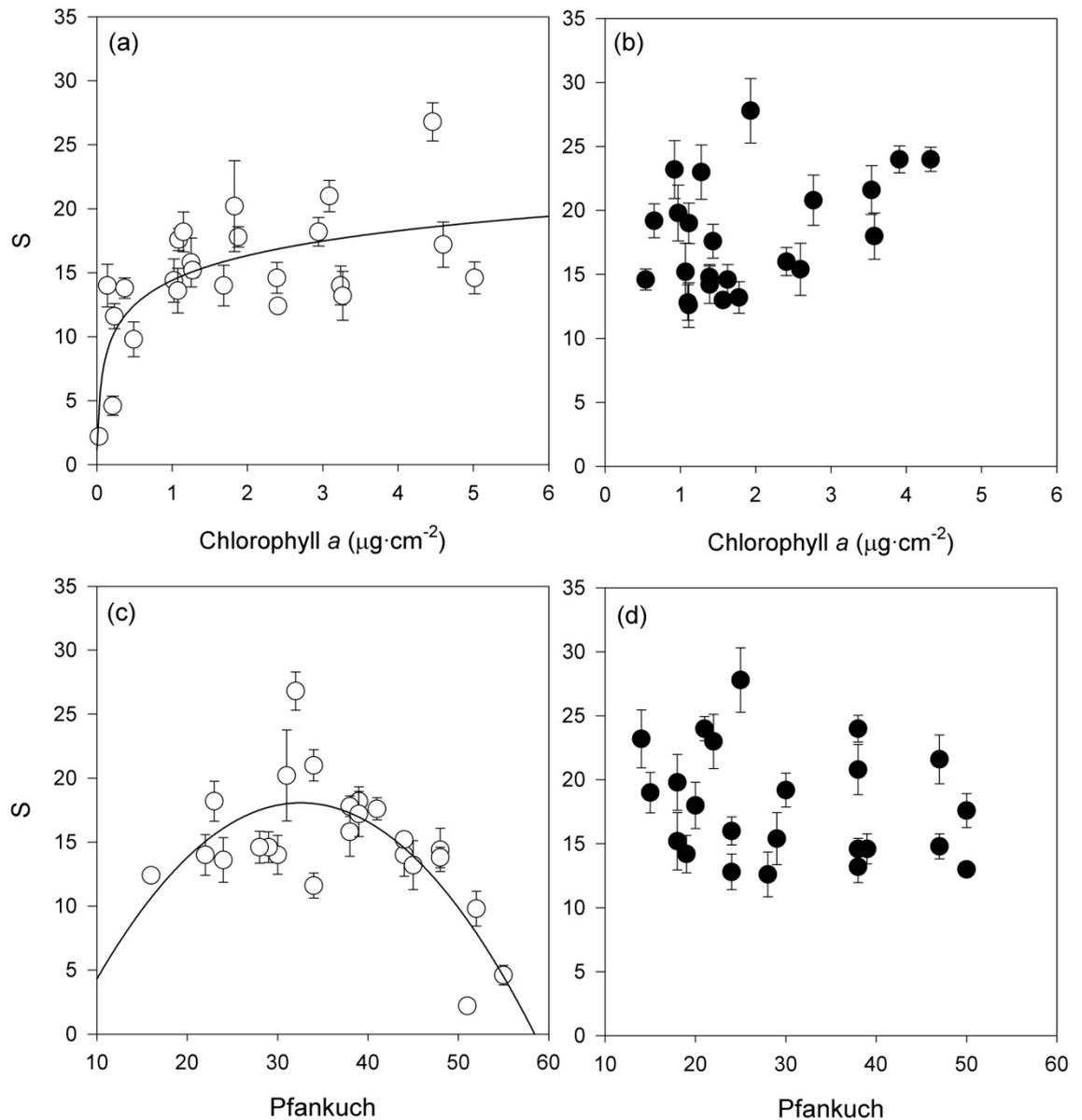


Figure 4: Mean (± 1 S.E.) number of taxa as a function of (a, b) chlorophyll *a* and (c, d) bottom component of Pfankuch stability index collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007. (a, c) Open canopy sites and (b, d) sites with canopy cover. See Table 2 for regression results.

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

Model testing

Fitting all sites to the DEM ($S = b_0 + b_1P + b_2C + b_3P^2 + b_4C^2 + b_5PxC$) explained 42 % of the variation in the data ($F_{5,41} = 5.84$, $P = 0.0004$, $r^2 = 0.42$; Fig. 5; 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. 6; Table 3) with only the Pfankuch and Pfankuch² 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 ($S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2 + b_4PxC$), explained 70 % of the variation in the open canopy data ($F_{4,19} = 11.21$, $P < 0.0001$, $r^2 = 0.70$; Fig. 6; 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. 5; Table 3). However, the interaction between productivity and disturbance in both the open canopy sites and the all sites set was not significant. There was no fit at the sites with canopy cover ($F_{5,17} = 2.41$, $P = 0.09$, $r^2 = 0.35$).

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. 6; 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. 5; Table 3), and did not fit at sites with canopy cover ($F_{5,17} = 1.69$, $P = 0.2$, $r^2 = 0.21$).

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 ($S = b_0 + b_1P + b_2C + b_3P^2 + b_4C^2 + b_5PxC$), (b) model 1 – with productivity x disturbance interaction ($S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2 + b_4PxC$) and (c) model 2 – without productivity x 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 sites		
	Coefficient (SE)	t	P	Coefficient (SE)	t	P
(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

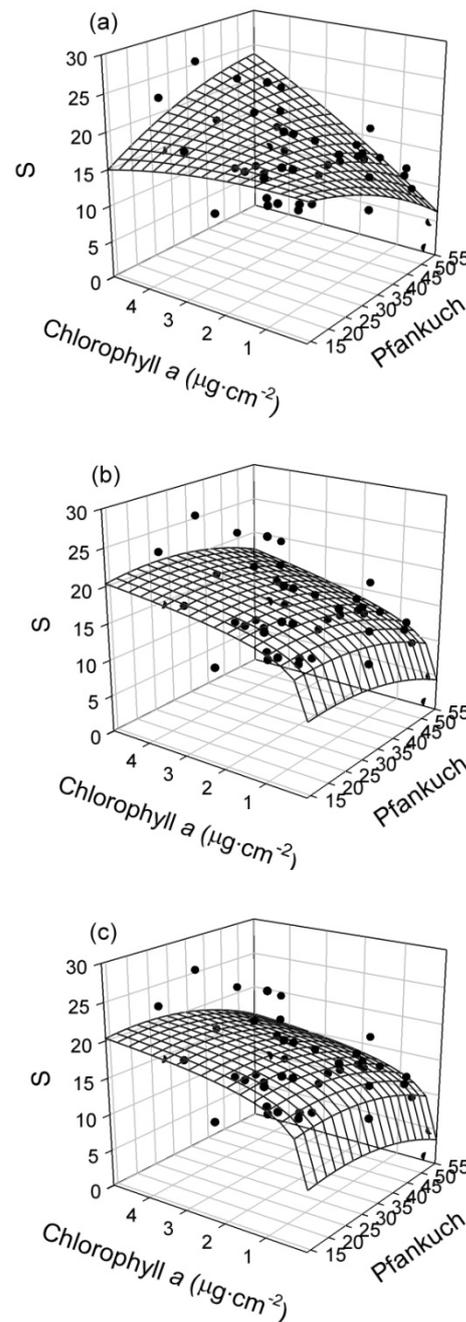


Figure 5: Taxonomic richness as a function of chlorophyll *a* and the bottom component of the Pfankuch stability index for open sites and sites with canopy cover collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007. (a) DEM ($S = b_0 + b_1P + b_2C + b_3P^2 + b_4C^2 + b_5PxC$), (b) model 1 – with productivity x disturbance interaction ($S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2 + b_4PxC$) and (c) model 2 – without productivity x 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.

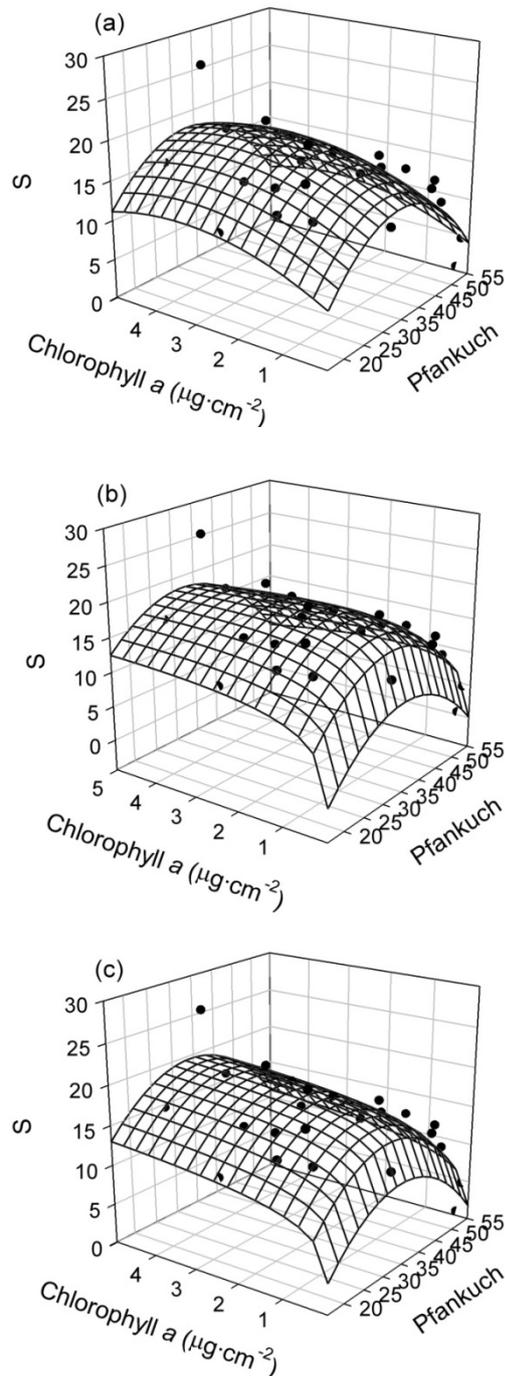


Figure 6: Taxonomic richness as a function of chlorophyll *a* and the bottom component of the Pfanckuch stability index for open canopy sites only collected from 47 streams in the Tongariro National Park, New Zealand, between February and April 2007. (a) DEM ($S = b_0 + b_1P + b_2C + b_3P^2 + b_4C^2 + b_5P \times C$), (b) model 1 – with productivity x disturbance interaction ($S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2 + b_4P \times C$) and (c) model 2 – without productivity x disturbance interaction ($S = b_0 + b_1P + b_2[\ln(C)] + b_3P^2$) where P = Pfanckuch and C = chlorophyll *a*. See Table 3 for coefficients and text for model fit.

Discussion

Although the DEM explained some of the variation in benthic invertebrate richness (42 % with all sites included), the underlying relationships did not entirely match those predicted by the DEM. Like Svensson et al. (2007), we found diversity peaked at intermediate levels of disturbance, measured here as stream bottom stability (Pfankuch index), irrespective of productivity level; matching the trend predicted by the IDH (Grime 1973b, Connell 1978, Sousa 1979). Whilst remaining a dominant paradigm in disturbance ecology, there has been limited support for the IDH in streams (but see Townsend et al. 1997) and less than 20 % support in all ecological studies testing this theory (Mackey and Currie 2001). Similarly, little evidence exists supporting the DEM in streams, although Cardinale et al. (2006) found support in primary producer communities in a wide variety of mid-Atlantic, North American streams. The only effect productivity had on this relationship in our study was in determining the magnitude of the peak of the richness curve.

The role of canopy cover

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 relationships found between open sites and sites with canopy cover. Previous studies have found that factors associated with canopy cover can alter the effects of floods on stream invertebrate communities (likely through the limitation of available light) (Robinson and Minshall 1986, Death 2002, Death and Zimmermann 2005, Fuller et al. 2008). Most of these studies also 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 and Zimmermann 2005,

Fuller et al. 2008). In the absence of canopy, periphyton is the dominant food source for invertebrates in stony streams whereas under canopy it is one of several potential food sources. Thus invertebrates would be expected to respond more strongly to algal productivity gradients in open canopy streams, rather than 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 and Zimmermann 2005). As such, in streams with canopy cover where periphyton resources are low, rate of recovery will be independent of algal productivity. Fuller et al. (2008) also suggest that when periphyton recovery is not limited by nutrients, open canopy stream invertebrate communities are more resilient to disturbances. The streams in this study are likely to be nutrient limited as they are pristine mountain streams 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 and Fegley 1989, Winterbourn 1990, Death and Zimmermann 2005), there was no effect of canopy cover on productivity in the streams studied here. This may be due to recent unrecorded disturbance events removing periphyton biomass although this was not evident in the time leading up to sampling (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 sites but not at sites with canopy cover. This may be due, in part, to the fact that the sites with canopy cover were more stable than the open sites, potentially due to stabilisation of river banks by riparian trees. Fuller et al. (2008) suggest that canopy cover may lead to communities more resistant to pulsed disturbances as long as organic matter is retained during floods or that as much organic matter is washed in as is washed out. We found no relationship between stability and CPOM, or between CPOM and invertebrate community diversity. We did not measure FPOM, which is generally considered

unimportant in New Zealand streams (Scrimgeour and Winterbourn 1989, Death and 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 and Winterbourn 1989, Death and Zimmermann 2005). This may be a result of the comparatively low level of allochthonous material entering or being retained in New Zealand streams which in turn causes a distinct lack of obligate shredders (Winterbourn et al. 1981, Winterbourn 1997). Lack of trophic specialisation in New Zealand stream invertebrates generally, and the dependence on a trade-off between traits such as competitive and colonising ability (Chesson and Huntly 1997, Roxburgh et al. 2004, Cadotte 2007), makes the task of fitting models to these communities a challenge.

Specific effects of disturbance and productivity

As noted earlier, diversity peaked at intermediate levels of disturbance as predicted by the 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 or absent, disturbance may simply be resetting the colonisation process by removing animals and their resource supply (Death 2002). This has been shown in streams with productivity setting the upper limit to richness rather than leading to competitive exclusion, and in turn leading to a different relationship to that predicted by the DEM (Death 2002). Evidence from our study suggests that disturbance is acting along the lines of the DEM/IDH by maximising richness at intermediate levels of disturbance. However, no taxa demonstrated strong trends for either end of the disturbance continuum; what appears to be evident is a large proportion of taxa are common at intermediate disturbance sites but less so at either stable or unstable sites. The few taxa to demonstrate any relationship were the midges *Maoridiamesa* spp. and one species of Orthocladiinae, and the calocid 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 due to a competitive hierarchy. For example, *Zelolessica 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 and Death 2006). Sites with much higher proportion of bryophyte cover can exclude other non-specialised taxa such as the commonly widespread *Deleatidium* (Suren 1991).

Given that most stream insects are highly mobile organisms, we would expect a unimodal relationship with disturbance to be less likely than if we were dealing with sessile organisms (Wootton 1998). Previous studies have shown that stream invertebrate diversity declines with increasing rates of disturbance (Death and Winterbourn 1995, Death 2002). Due to the nature of streams, and the lack of evidence to suggest competitive exclusion occurs in these systems, we feel Death's (Death 2002) assertion that disturbance acts by resetting the colonisation process holds more theoretical application in this situation.

The DEM predicts diversity will be maximised at intermediate levels of productivity; however, in the present study, richness and density both increased logarithmically with increasing rates of 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). When accounting for evenness, diversity (Simpson's) was not related to productivity. Both unimodal (e.g. Grime 1973a, Huston 1979, Rosenzweig 1992, 1995, Leibold 1999, Waide et al. 1999, Mittelbach et al. 2001) and linear (e.g. Currie and Paquin 1987, Currie 1991, Abrams 1995, Waide et al. 1999, Gaston 2000, Mittelbach et al. 2001) relationships have been found between productivity and diversity (Abrams 1995, Waide et al. 1999, Mittelbach et al. 2001). One possible explanation for the non-uniform responses may be the scale at which a system is observed (Chase and 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.

Interactions between productivity and disturbance

Both the DEM and our model had no interaction term between productivity and stability. 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. Haddad et al. (2008) suggests it is not necessarily a competition colonisation trade-off but intrinsic growth rates of species that is more important for the response to disturbance.

Productivity can help to explain the contrasting responses of diversity to disturbance in ecological communities (Huston 1979, Kondoh 2001), but the model we developed here simply suggests that, rather than shifting the peak in diversity, productivity logarithmically increases the magnitude of the unimodal disturbance-diversity curve. Essentially richness peaks at intermediate levels of disturbance with productivity determining the magnitude of that peak. Without the interaction between disturbance and productivity we cannot unequivocally suggest that disturbance not only acts directly upon invertebrates but on their food supply, as suggested by Death (2002) and Death and Zimmerman (2005). This lack of interaction was surprising for two reasons. Firstly, theoretically these should go hand-in-hand with disturbances creating niches and productivity controlling the rate of colonisation. Secondly, although important, we believe 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).

This study was conducted in low nutrient streams where the range of productivity was limited and therefore the results only represent part of the productivity gradient found in nature. Alpine streams are often characterised by low

productivity and instability (Milner and Petts 1994, Gafner and Robinson 2007). In fact, nutrient enrichment in alpine streams can alter the response of stream invertebrate communities to disturbance (Robinson and Minshall 1986, Gafner and Robinson 2007). Thus it is important to carefully consider the range of productivities encompassed in any study (Scholes et al. 2005). Perhaps the crux of the issue here is that we only encountered the lower end of the scale on the productivity continuum for assessing the DEM. Consequently, the logarithmic increase in richness with productivity we found may merely be the peak in a greater unimodal relationship and an interaction between productivity and disturbance may well occur. Furthermore, the relationship between productivity and richness is highly variable at smaller spatial scales (Mittelbach et al. 2001, Field et al. 2009).

Conclusions

In summary, we found little evidence to support the DEM within the range of conditions encountered, and there was no indication of competitive displacement at higher levels of productivity as predicted by the DEM. Although productivity and disturbance were shown to be important determinants of richness, we suggest that they act independently of each other and are not sufficient to explain patterns in these mountain streams in isolation of other factors. It appears more complex multivariate models than those such as the DEM are required to adequately explain diversity in these natural systems. Although the DEM and our model were sufficient in predicting diversity in the absence of canopy cover, where canopy was present their success in predicting diversity was extremely limited. 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.

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Chapter 3

Consistent effects of productivity and disturbance on diversity between landscapes



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 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 favourable 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 responded log-linearly 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 the Death productivity-disturbance-diversity is the most applicable model in these communities where disturbance simply removes taxa and productivity controls the upper limit to richness.

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 hypothesised 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. Wilson and Tilman 2002, 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. 2005, Death and Zimmermann 2005, 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 quite how diversity responds to productivity and disturbance. Streams provide a unique testing ground for these models because community dynamics are dominated by immigration and emigration rather than population growth for which most theoretical and empirical work in this field has been applied. Many of the assumptions of the major diversity models are not met in lotic communities which are dominated by highly mobile taxa (Hildrew and Giller 1994, Allan 1995) rather than sedentary organisms such as plants and corals for which many of these models have been developed.

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 colonisation 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. (In prep.) 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 (Wilson and Tilman 2002, 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. (In prep.), 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 recolonisation after disturbance that there should be significant interaction terms.

Habitats worldwide are under threat from increasing land use intensification (Tilman 1999b, 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). These changes can lead to a subsidy-stress response of communities where the initial response may be positive but becomes negative at greater rates of environmental change (Quinn 2000, Niyogi et al. 2007, Death and Collier 2010). 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.

The effects of catchment land use on the response of stream invertebrate communities to flow disturbance are not well documented. 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 investigate whether the effects of productivity and disturbance on diversity differ between a pristine and non-pristine agricultural region by sampling 16 streams on multiple occasions in the North Island of New Zealand. In order to do

this we 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 (In prep.) version of this model. Based on Tonkin et al. (In prep.) 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 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

The Tongariro National Park, in the North Island central plateau of New Zealand, is a world heritage site dominated by a central volcanic massif. Rainfall ranges from 1,100-3,500 mm yr⁻¹ 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 characterised by a warm and dry climate with a mean annual rainfall of 783 mm in the central Ruataniwha Plains. Eight streams were sampled in each of these two regions which were selected to represent a pristine (Tongariro) and non-pristine (Hawke's Bay) region. Study sites were selected to represent high and low productivity in stable and unstable streams in each region. 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). Figure 1 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 m² 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).

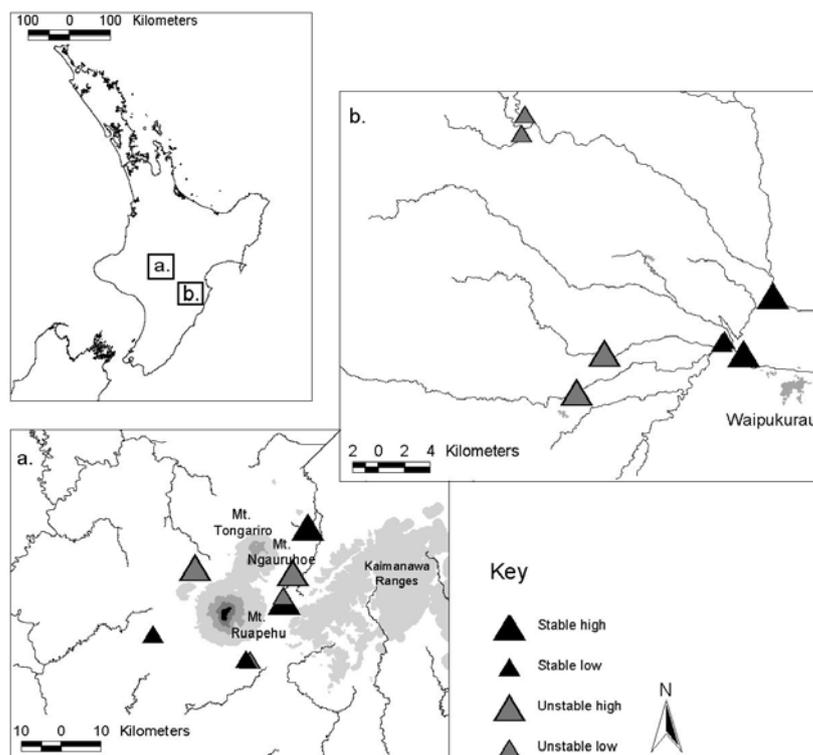


Figure 1: Map showing location of the 16 study sites in two regions of the North Island of New Zealand collected on four occasions between February 2008 and July 2009. a. Tongariro National Park (pristine) and b. Hawke's Bay (non-pristine). The key shows the difference between stable and unstable and low and high productivity sites based on *a priori* selection.

Periphyton

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 mm x 45 mm tiles were attached to one 500 mm x 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*. 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 (α 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 and using Graham et al. (1988) and halved to account for periphyton being present only on stone surfaces.

Measurement of disturbance

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 (Winterbourn and Collier 1987, 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). 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

Substrate size composition was assessed using the 'Wolman Walk' method where the β 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 (Quinn and Hickey 1990). 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 standardising 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, U.S.A.). 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 normalise the data. To visualise differences in community structure between the two regions and between productivity and disturbance 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. (In prep.) 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 form:

1. DEM

$$S = b_0 + b_1D + b_2C + b_3D^2 + b_4C^2 + b_5DxC$$

2. Death model without interaction between productivity and disturbance

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

3. Death model with interaction between productivity and disturbance

$$S = b_0 + b_1D + b_2[\ln(C)] + b_3DxC$$

4. Tonkin model without interaction between productivity and disturbance

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

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.

Results

Physical characteristics and disturbance

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

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. 2). Periphyton biomass declined with increasing bed disturbance (Fig. 2; Table 2). This trend was stronger at Hawke's Bay sites compared to Tongariro sites but the trend was the same (Fig. 2).

Table 1: 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. HB = Hawke's Bay (non-pristine), NP = Tongariro (pristine), alt. = altitude, cond. = conductivity, temp. = temperature, prod. = productivity.

Site	Location	Alt. (m)	Mean width (m)	Mean depth (cm)	Mean velocity (m s ⁻¹)	Mean cond. (μS cm ⁻¹)	Mean temp. (°C)	Mean % moved	Stability	Prod.
HB1	Makaroro River @ Makaroro Rd	312	5.7	17	0.3	93.3	12.7	95	Unstable	Low
HB2	Waipawa River @ Wakarara Rd	315	6.7	19.4	0.48	96.7	12.8	76.7	Unstable	Low
HB3	Spring creek @ Swamp Rd	146	4.7	43.6	1.52	170	13.7	3.3	Stable	High
HB4	Spring creek @ Lyndsay Rd	134	3.8	22	1.17	230	14.6	40	Stable	High
HB5	Makaretu River @ Burnside Rd	216	5.3	15.8	0.87	96.7	12.9	60	Unstable	High
HB6	Tukipo River @ Burnside Rd	191	7	15	0.2	150	15	30	Unstable	High
HB7	Spring 1 @ Ongaonga Waipuk. Rd	143	1.5	15.2	0.42	153.3	14.8	13.3	Stable	Low
HB8	Spring 2 @ Ongaonga Waipuk. Rd	139	3.2	75.6	0.07	110	15.5	0	Stable	Low
NP1	Wahianoa stream u/s intake	934	6.1	25.6	0.97	70	9.4	50	Unstable	Low
NP2	Unnamed Karioi forest stream	935	3.5	22.6	0.96	139.7	8.6	30	Stable	Low
NP3	Orautoha stream @ middle rd	712	2.5	24.4	0.55	92.7	8.2	8.3	Stable	Low
NP4	Whakapapaiti @ SH4	859	15.8	28.2	0.98	106	8.1	28.3	Unstable	High
NP5	Te Piripi stream @SH1	993	2.2	16.6	0.67	67.7	9.1	10	Stable	High
NP6	Mangatoetoenui @ SH1	971	9.4	44.2	0.96	133	9.5	25	Unstable	Low
NP7	Oturere Stream SH1	809	9.4	42.4	0.86	110.7	8.6	8.3	Unstable	High
NP8	Poutu Stream	518	7.7	43.6	1.05	70.3	8.9	8.3	Stable	High

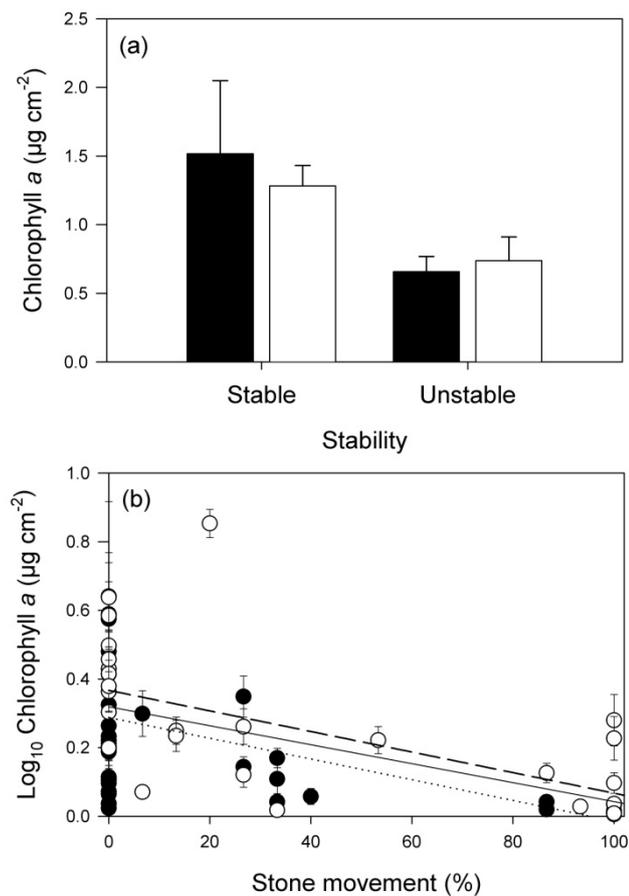


Figure 2: Mean chlorophyll *a* concentrations (± 1 S.E.) (a) for sites in each *a priori* selected stability group in both regions and (b) as a function of percent stone movement collected in 16 streams, North Island, New Zealand, February 2008-July 2009. Black bars/circles are pristine (Tongariro) and 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 2 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. 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 %).

Table 2: 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. D.f. = degrees of freedom. AIC = Akaike's information criterion where lower numbers represent a better model.

	D.f.	F (AIC)	P	r ²	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

NMDS (Fig. 3) and ANOSIM confirmed community structure differed between the two regions ($R = 0.42$, $P = 0.001$, Fig. 3), 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 ($R = 0.16$, $P = 0.001$, Fig. 3) and less so between low and high productivity sites ($R = 0.06$, $P = 0.017$, Fig. 3). 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.

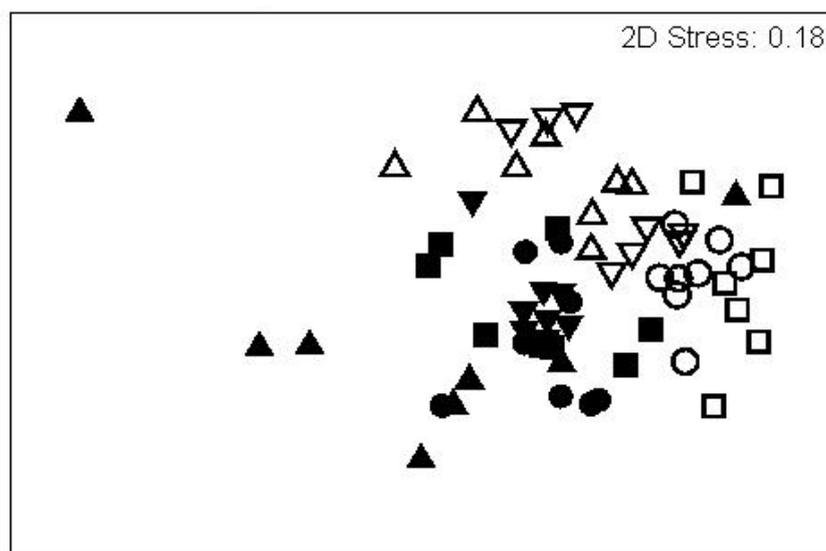


Figure 3: Non-metric multidimensional scaling (NMDS) ordination on $\log(x + 1)$ transformed data for 16 streams collected on four occasions between February 2008 and July 2009 in the North Island of New Zealand. Closed circles are pristine sites (Tongariro Region), open circles are non-pristine sites (Hawke's Bay region). Unstable/low productivity: upright triangles; Unstable/high productivity: inverted triangles; Stable/low productivity: squares; Stable/high productivity: circles.

Density and diversity

The density of invertebrates per 0.1 m² was significantly higher at Hawke's Bay streams with 603.93 individuals 0.1 m⁻² opposed to Tongariro's 253.58 individuals 0.1 m⁻² (Table 3). Density was significantly higher at stable than unstable streams, with 578.63 individuals 0.1 m⁻² at stable streams and 278.1 individuals 0.1 m⁻² at unstable streams (Table 3). There was no interaction between stability and region (Table 3). Density was significantly higher at high productivity sites with 515.8 individuals and 333.2 individuals at low productivity sites (Table 3). There was no interaction between productivity and stability nor was there a three way interaction including region (Table 3). Density increased logarithmically with increasing periphyton biomass and declined with increasing bed movement (Fig. 4; Table 2). 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. 4; Table 2).

Table 3: 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.

	No. of animals		No. of taxa		Rarefied richness (ES224)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
	Stability	18.19	0.0001	28.81	<0.0001	5.89
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 x productivity	7.79	0.007	11.31	0.001	3.91	0.053
Stability x region	0.38	0.54	1.95	0.17	2.37	0.13
Productivity x region	3.53	0.065	0.96	0.33	1.59	0.21
Stability x productivity x region	0.81	0.37	7.05	0.01	10.51	0.002

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 m⁻² and 14.57 taxa 0.1 m⁻² at Hawke's Bay streams; however, this was not a significant difference (Table 3). Richness was higher at stable sites with 18.11 taxa 0.1 m⁻² and 12.07 taxa 0.1 m⁻² at unstable sites (Table 3). Richness was higher at high productivity sites with 17 taxa and 13 at low productivity sites (Table 3). Productivity and stability interacted to effect richness and there was also a three-way interaction between productivity, stability and

region (Table 3). Taxonomic richness increased logarithmically with increasing periphyton biomass and declined with decreasing bed stability (Fig. 5; Table 2). These trends were consistent for both regions but the fit of both models was greater at Hawke's Bay sites (Fig. 5; Table 2).

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 3). 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 (Table 3). There was no interaction between region and stability, but productivity and stability did interact with region (Table 3). Rarefied richness declined gradually with increasing bed movement (Fig. 6; Table 2). When fitting to each individual region, no relationship was found between bed movement and rarefied richness at Tongariro sites (Fig. 6; Table 2). There was no relationship between periphyton biomass and rarefied richness at all sites (Fig. 6; Table 2).

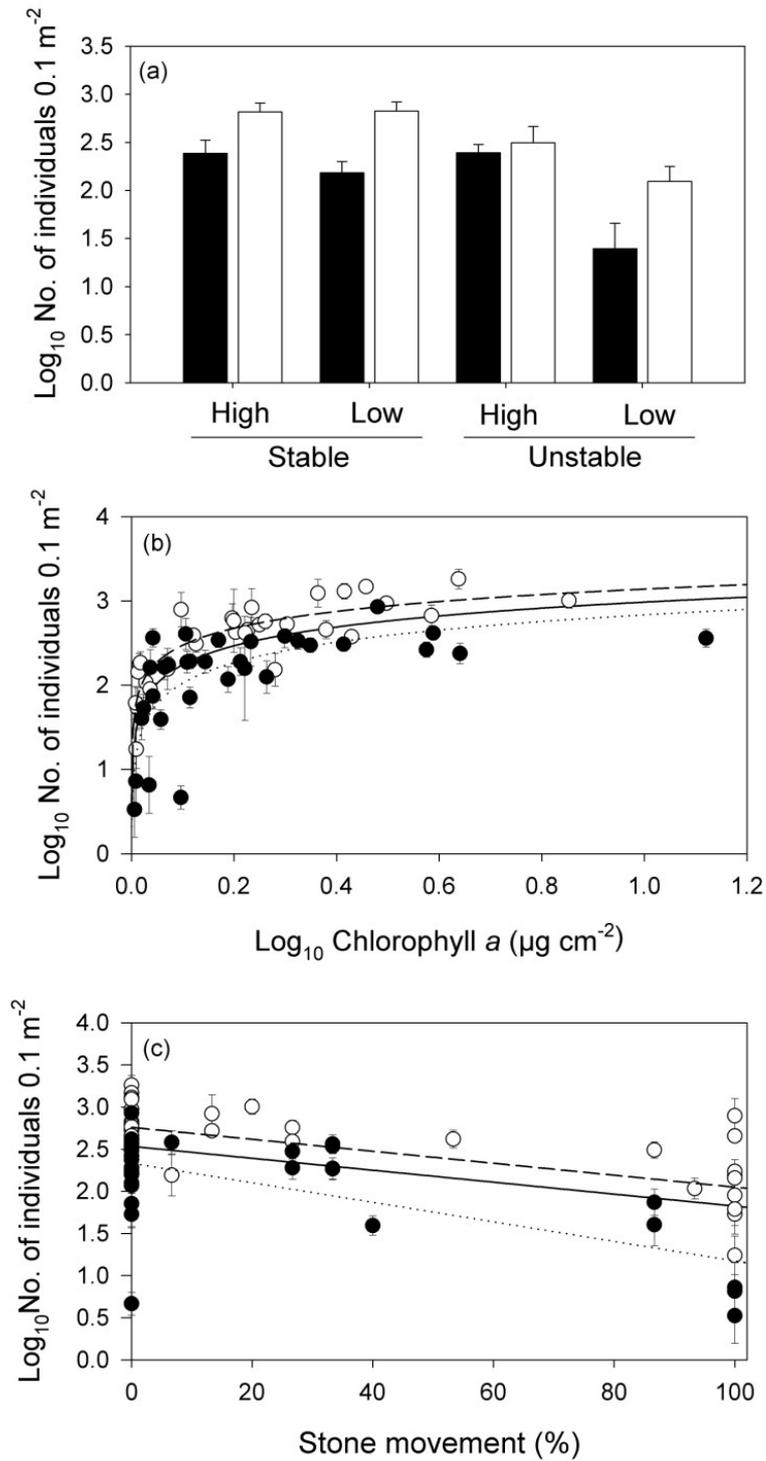


Figure 4: Mean number of animals (± 1 S.E.) collected in 16 North Island, New Zealand streams on four occasions between February 2008 and July 2009. (a) For each *a priori* selected stability and productivity group, (b) as a function of mean chlorophyll *a* and (c) as a function of percent stone movement. 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 3 for ANOVA results and Table 2 for regression results.

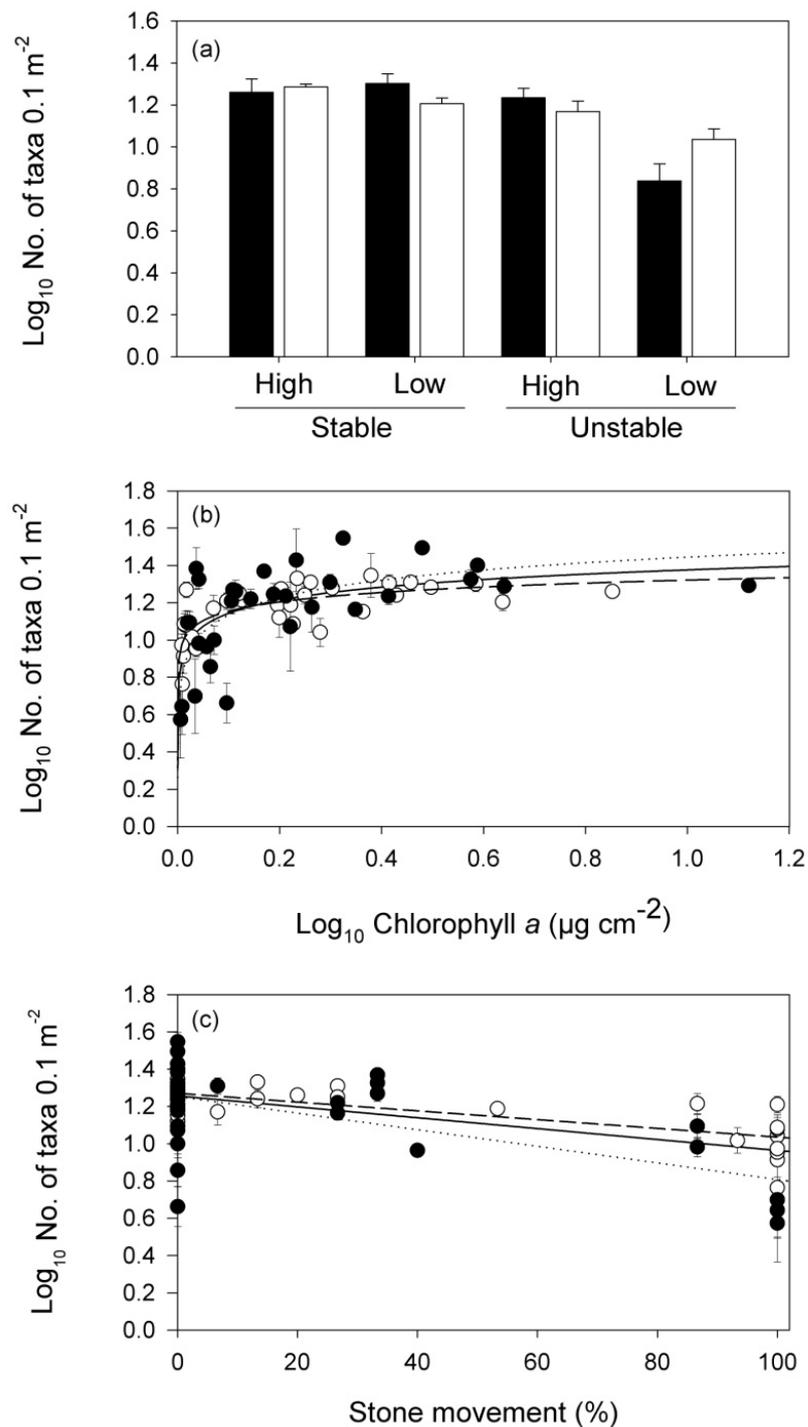


Figure 5: Mean number of taxa (± 1 S.E.) collected in 16 North Island, New Zealand streams on four occasions between February 2008 and July 2009. (a) For each *a priori* selected stability and productivity group, (b) as a function of mean chlorophyll *a* and (c) as a function of percent stone movement. 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 3 for ANOVA results and Table 2 for regression results.

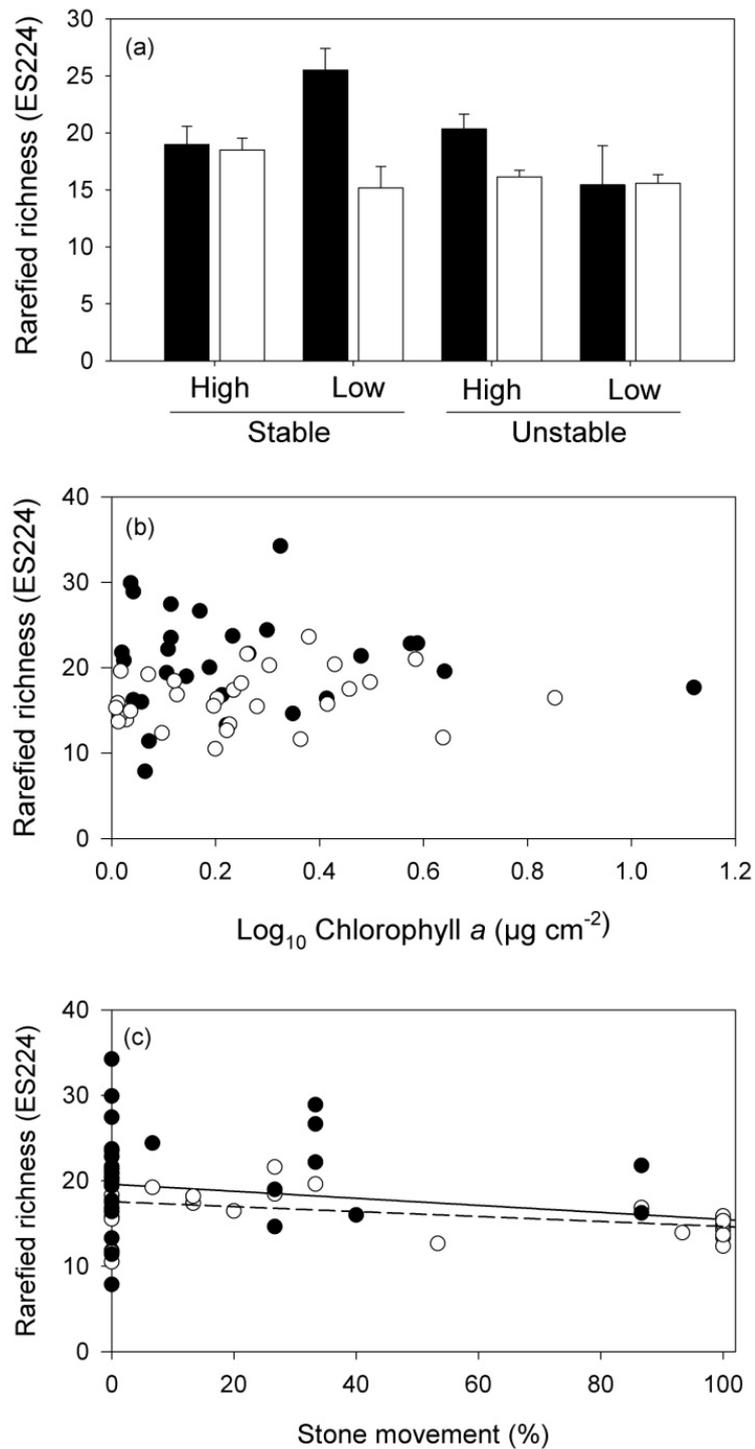


Figure 6: (a) Mean rarefied richness (± 1 S.E.) calculated for 224 individuals collected in 16 North Island, New Zealand streams on four occasions between February 2008 and July 2009 for each *a priori* selected stability and productivity group. (b) Pooled rarefied richness calculated for 224 individuals as a function of mean chlorophyll *a* and (c) as a function of percent stone movement. 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 3 for ANOVA results and Table 2 for regression results.

Model fitting

All five models explained a large proportion of the variation in taxonomic richness at all sites (Fig. 7; Table 4; Table 5). The DEM explained 50.9 % of the variation in the data for the number of taxa (Fig. 7; Table 4). 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 (Fig. 7; Table 4). The Death model explained 47.9 % of the variation with and without the interaction between productivity and disturbance included (Fig. 7; Table 4). 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 (Fig. 7; Table 4). 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. 7; Table 5). The productivity coefficients were significant throughout all five models whereas the only significant disturbance coefficients were the disturbance² 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. 7; Table 4). 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 ($0.48 < r^2 < 0.52$) (Fig. 7; Table 4).

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. 7; Table 4). However, model fit was consistently better in the non-pristine sites than the pristine sites (Fig. 7; Table 4). Although the DEM did explain a large proportion of the variation, AIC indicated it was the least likely model for these data (Fig. 7; Table 4). The pristine region responded differently to the three models with the productivity-disturbance interaction (Fig. 7). The two models with the interaction and a quadratic relationship between disturbance and diversity suggested diversity at the pristine sites would decline significantly at high levels of disturbance and productivity (Fig. 7).

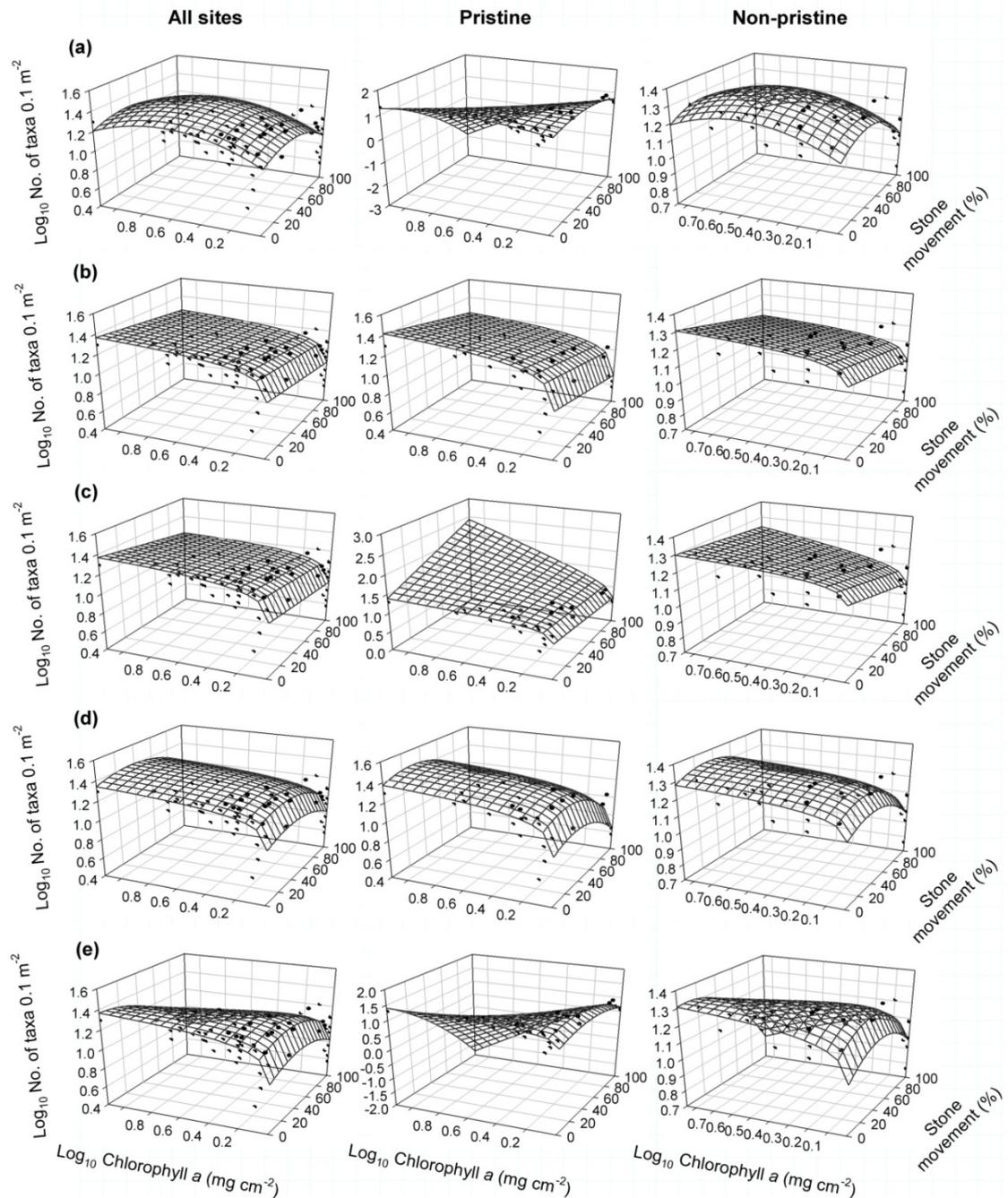


Figure 7: Model fit for mean number of taxa collected from 16 North Island, New Zealand sites on four occasions between February 2008 and July 2009 with all sites included, pristine only (Tongariro) and non-pristine only (Hawke’s Bay) sites. (a) DEM, (b) Death model – no P x D (productivity x disturbance) interaction, (c) Death model – with P x D interaction, (d) Tonkin model – no P x D interaction, and (e) Tonkin model – with P x D interaction. See Table 4 for model fit results and Table 5 for model coefficients.

Table 4: 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. With interaction indicates the productivity x 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.

	D.f.	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	-97.9
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	0.6	-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	9.4	<0.0001	0.17	0.58	-39.17
c) Non-pristine						
DEM	5, 25	11.58	<0.0001	0.08	0.7	-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	0.7	-59.82
Tonkin (with interaction)	4, 26	16.51	<0.0001	0.08	0.72	-58.41

Table 5: 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. With interaction indicates the productivity x disturbance interaction term is included in the model. D = disturbance and P = productivity.

	All sites			Pristine			Non pristine		
	Coefficient (S.E.)	<i>t</i>	<i>P</i>	Coefficient (S.E.)	<i>t</i>	<i>P</i>	Coefficient (S.E.)	<i>t</i>	<i>P</i>
DEM									
y0	1.07 (0.06)	18.14	<0.0001	1.03 (0.08)	13.13	<0.0001	1.11 (0.08)	13.28	<0.0001
D	0.004 (0.003)	1.55	0.13	0.01 (0.006)	1.75	0.092	0.004 (0.003)	1.49	0.148
P	0.79 (0.28)	2.82	0.007	1.06 (0.42)	2.54	0.017	0.65 (0.36)	1.79	0.086
D ²	-0.00006 (0.00002)	-2.44	0.017	-0.0001 (0.00001)	-2.38	0.025	-0.0001 (0.00002)	-2.4	0.024
P ²	0.6 (0.28)	-2.17	0.034	-0.76 (0.4)	-1.91	0.067	-0.65 (0.38)	-1.73	0.095
DxP	0.0001 (0.005)	0.02	0.98	-0.03 (0.02)	-1.02	0.32	-0.0004 (0.004)	-0.12	0.91
Death									
y0	1.36 (0.04)	37.99	<0.0001	1.41 (0.07)	20.63	<0.0001	1.31 (0.03)	46.71	<0.0001
D	-0.001 (0.0006)	-2.01	0.049	-0.002 (0.001)	-1.46	0.16	-0.002 (0.001)	-2.87	0.008
P	0.07 (0.02)	3.83	0.0003	0.1 (0.04)	2.7	0.011	0.04 (0.02)	2.36	0.025
Death (with interaction)									
y0	1.36 (0.05)	29.78	<0.0001	1.38 (0.08)	17.91	<0.0001	1.3 (0.04)	30.93	<0.0001
D	-0.001 (0.0009)	-1.31	0.19	-0.003 (0.002)	-1.55	0.13	-0.002 (0.001)	-1.78	0.087
P	0.08 (0.03)	2.92	0.005	0.09 (0.04)	2.25	0.033	0.03 (0.03)	1.13	0.27
DxP	-0.0003 (0.005)	-0.06	0.95	0.01 (0.02)	0.62	0.54	0.001 (0.004)	0.3	0.77
Tonkin									
y0	1.34 (0.04)	36.88	<0.0001	1.37 (0.07)	19.9	<0.0001	1.25 (0.03)	40.64	<0.0001
D	0.004 (0.002)	1.56	0.12	0.005 (0.004)	1.27	0.22	0.002 (0.03)	0.98	0.33
P	0.07 (0.02)	3.86	0.0003	0.09 (0.04)	2.49	0.019	-0.002 (0.07)	-0.02	0.98
D ²	-0.00005 (0.00002)	-2.21	0.031	-0.0001 (0.00004)	-1.92	0.065	-0.00004 (0.00002)	-2.13	0.042

Table 5 continued....

	All sites			Pristine			Non pristine		
	Coefficient (S.E.)	t	P	Coefficient (S.E.)	t	P	Coefficient (S.E.)	t	P
Tonkin (with interaction)									
y0	1.36 (0.04)	30.8	<0.0001	1.39 (0.07)	19.07	<0.0001	1.32 (0.04)	34.31	<0.0001
D	0.005 (0.003)	1.76	0.083	0.01 (0.01)	1.63	0.115	0.01 (0.003)	1.92	0.067
P	0.09 (0.03)	3.43	0.001	0.1 (0.04)	2.72	0.011	0.07 (0.03)	2.31	0.029
D ²	-0.00006 (0.00002)	-2.36	0.022	-0.0001 (0.0001)	-2.11	0.045	-0.0001 (0.00002)	-2.68	0.013
DxP	-0.005 (0.005)	-0.84	0.4	-0.03 (0.03)	-1.08	0.29	-0.005 (0.005)	-1.08	0.29

Discussion

Diversity of invertebrate communities responded strongly to both productivity and disturbance in this study. We found evidence to support Death's (2002) productivity-disturbance-diversity model in these streams. Our results suggest Huston's (1979, 1994) DEM is not applicable in these streams. However we also found support for Tonkin et al.'s (In prep.) modification of the Death model of diversity to include a quadratic disturbance-diversity relationship. There was little difference in the way in which productivity and disturbance affected diversity between the pristine and non-pristine regions. Curiously, 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).

Regional differences

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 urbanisation (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 destabilised 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, Tschardt 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 response to 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 colonisation processes at a regional scale which may in turn generate local processes such as competition (Tilman 1999a, 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 loose and thus diversity may have been affected more than the measured movement indicates.

Model fitting

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 favourable 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 significant. While our data fit slightly better to the model of Tonkin et al. (In prep.), the difference in strength of fit was negligible. The only difference between the models put forward by Death (2002) and

Tonkin et al. (In prep.) 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. (In prep.) 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 (Connell 1978), 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 levels.

Like Tonkin et al.'s (In prep.) 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 (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. (In prep.) 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.

As hypothesised, we found little evidence to suggest the DEM applies in these streams. 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 controlled 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 (Williams and Hynes 1976, 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 monopolise 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 levelling 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 recolonisation (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 recolonisation 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. (In prep.) 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 don't 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 Zimmerman (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 response of rarefied richness to 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. Essentially, more resources will likely lead to more individuals per species while more taxa are likely to appear when a greater diversity of resources is present rather than a greater volume of resources.

Conclusions

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. In prep.). We found little evidence to support the DEM (Huston 1979, 1994), and found 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 response of diversity to productivity and disturbance 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. (In prep.) model are applicable to ecological communities with highly mobile animals irrespective of the landscape they are applied within.

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Chapter 4

Productivity-diversity relationships in streams and the role of periphyton assemblages



Abstract

There is much debate as to what the form of the productivity-diversity relationship is, particularly in lotic systems which have received few assessments of this relationship. One factor that assessments of primary productivity do not account for is the growth form of algae that drives production. Thus, we set out to (i) examine the productivity-diversity relationship in 24 streams of Cantabria, Spain, in July 2007 and (ii) determine whether this relationship was underpinned, and better explained, by specific responses to the form of the periphyton community. Due to recent evidence in streams suggesting productivity simply sets the upper limit to richness, rather than to increase the effect of competitive interactions, we hypothesized that diversity would be a log-linear function of productivity. We predicted that diversity would respond oppositely to two coarse measures of the periphytic community; i.e., positively to % diatom cover and negatively to % filamentous algae cover. There was no relationship between productivity and diversity in these streams but, as predicted, this relationship was underpinned by responses to the growth form of periphyton community. Diatom cover was the best predictor of invertebrate diversity patterns. Generally, diversity responded positively to % diatom cover and negatively to % filamentous algae cover. However, results were variable and % EPT exhibited a greater sensitivity to higher levels of diatom cover. These findings highlight two important implications: firstly, productivity-diversity relationships in streams can be underpinned by interactions with specific forms of periphyton. Secondly, rapid assessment of periphytic forms is useful for managers as these coarse measures are highly relevant to higher trophic levels. We suggest a threshold of 40 % filamentous algae cover for managers wishing to minimise deleterious effects of eutrophication on stream communities.

Introduction

Although the relationship between productivity and diversity is a central theme in ecological research (Currie 1991, Abrams 1995, Waide et al. 1999, Mittelbach et al. 2001), we are far from reaching a consensus on the form of the relationship either empirically or in theory (Waide et al. 1999, Mittelbach et al. 2001). Unimodal (e.g. Grime 1973, Huston 1979, Rosenzweig 1992, 1995, Leibold 1999, Waide et al. 1999, Mittelbach et al. 2001) and linear (e.g. Currie and Paquin 1987, Currie 1991, Abrams 1995, Waide et al. 1999, Gaston 2000, Mittelbach et al. 2001) increases in diversity with increasing productivity prevail as the most common forms of this relationship. Differences in the observed patterns may be a result of several factors including the spatial scale of observation (Currie 1991, Mittelbach et al. 2001, Chase and Leibold 2002), disturbance (Huston 1979, 1994), and history of community assembly (Fukami and Morin 2003). However, the relationship has also been shown to differ between ecosystems and organisms studied (Waide et al. 1999, Mittelbach et al. 2001). These differences suggest individual patterns are driven by underlying ecosystem specific interactions. Furthermore, the methods used to collate the information on the productivity-diversity relationship have recently come under heavy criticism due to inconsistent classification and errors in meta-analyses (Hillebrand and Cardinale 2010, Whittaker 2010).

While abiotic forces (floods, hurricanes etc.) are considered to dominate biotic forces (competition, predation) in many systems, plant-herbivore relationships remain the basis of most ecosystems. As such the control of diversity is likely to be an interaction between disturbance and the productivity of an ecosystem (Huston 1979, 1994, Kondoh 2001). No system is more heavily influenced by regular disturbance events than streams (e.g. flooding) (Resh et al. 1988, Lake 2000, Death 2008). Death (2002) suggests that floods remove taxa and their resources and opens the habitat for recolonisation whilst primary productivity sets the upper limit to how many animals can return to these habitats after the disturbance. Recent support has been found for Death's hypothesis but these studies found no evidence of interactive effects of disturbance and productivity (Tonkin and Death In prep., Tonkin et al. In prep.), but

rather that diversity is a result of the additive effects of disturbance and productivity. Without the interactive effects of disturbance, making sense of the productivity-diversity relationship in streams should be clear-cut. However, compared to lentic systems and in fact most other environments, few studies have investigated whether higher productivity leads to greater diversity in lotic systems. The few to look specifically at this have found both unimodal (Death and Zimmermann 2005) and log-linear (Death 2002, Barquin 2004, Tonkin and Death In prep., Tonkin et al. In prep.) increases in diversity with productivity.

Assessing the relationship between primary productivity and diversity is essentially testing the response of higher trophic levels to the rate of energy production at lower trophic levels. Primary productivity is typically provided in streams by periphytic algae. Algal forms vary greatly in streams from prostrate and stalked diatoms through to filamentous green algae (Allan 1995), all of which respond differently to environmental conditions. It is now common practice to use the periphyton community as an index for biomonitoring environmental conditions (Kelly and Whitton 1995, Pan et al. 1996, Kelly 1998b, a, Kelly and Whitton 1998, Hill et al. 2000). Typically the focus of these assessments of biotic integrity have been diatoms (Kelly and Whitton 1995, Pan et al. 1996, Kelly 1998b), but Whitton and Kelly (1995) advocated the use of the full community of plants including bryophytes.

Not only do various forms of periphytic algae respond differently to environmental conditions but they can provide diverse habitat and resources for higher trophic levels. Different periphyton growth forms can also fulfil different functional roles in benthic communities (Steinman et al. 1992). When levels of periphyton reach greater densities and epilithic diatoms are replaced by macroalgae such as filamentous green algae, interactions between grazers and periphyton can shift from simple plant-herbivore interactions to more complex relationships. As well as providing food for a few specialist taxa, macroalgae can both provide and remove habitat and compete for space with invertebrates. Dudley et al. (1986) classed invertebrates into those negatively affected by macroalgae due to competition for space, positively affected due to habitat provision, and positively affected by food provision. This can be reflected in the typical shift from pollution (nutrient) sensitive

taxa associated with thin diatom films, to pollution tolerant taxa and filamentous algae growth forms often associated with nutrient eutrophication (Suren et al. 2003). Of course, grazing can have a large impact on periphyton in aquatic systems and this top-down control has been the central focus of periphyton-invertebrate community relationships to date (Hillebrand 2009). This grazing control can differ between growth forms of periphyton (Feminella and Hawkins 1995), such as that between diatom and filamentous forms (Suren and Riis 2010). Lamberti (1989) suggests this differential response of algae may initially occur where productive capacity of algae is high, but may be later regulated through the arrival of specialist grazers, or physical disturbance (Fisher et al. 1982). This indicates that vigilance is needed when inferring top-down or bottom-up control as it is likely to change through time and may be dependent on animals present in the system at hand.

Compared to other ecosystems, the productivity-diversity relationship has received relatively little attention from lotic ecologists. Thus, we set out to (i) test the response of stream invertebrate diversity to primary productivity; and (ii) because productivity measurements do not account for variation in the form of producers, we examine if this productivity-diversity relationship can be better explained by underlying responses to different forms of periphyton (i.e. diatoms/periphytic mats and filamentous green algae). We also use a common stream specific metric, % EPT, to assess whether this metric is more sensitive to environmental gradients in streams than simple diversity measures. As a result of previous work in streams (Death 2002, Barquin 2004, Tonkin and Death In prep., Tonkin et al. In prep.), and the fact that productivity does not appear to increase rates of competitive exclusion in streams as it often does in lakes, we hypothesise that diversity will increase logarithmically with increasing productivity. However, we predict that this relationship will be underpinned by particular responses to different forms of periphyton. Specifically, due to the view that diatoms are considered favourable to grazers and filamentous algal forms poor habitat for many invertebrates (Suren and Riis 2010), diversity will respond positively to % diatom cover and negatively to % filamentous algae cover.

Methods

Study sites

Twenty four streams were sampled in the Cantabrian Mountains of Northern Spain (Fig. 1, Appendix 1). The Cantabrian Mountains span ~483 km east to west along the northern coast of Spain reaching 2,648 m asl at Torre de Ceredo. Average rainfall ranges from ~1,200 to 1,600 mm p.a. depending on location within the region. Land-use surrounding sampling sites varied from Atlantic deciduous forest consisting predominantly of oak (*Quercus* spp.) and European beech (*Fagus* spp.) to pasture and small urban settlements. Sites were selected from six river catchments: Rio Besaya, Rio Saja, Rio Pas, Rio Pisueña, Rio Nansa, and Rio Ebro. Within each catchment sites were selected *a priori* so that one low and one high productivity site in close geographic proximity were sampled. As these were selected prior to sampling, productivity estimates for the selection of *a priori* high and low productivity streams were based on visual estimates of periphyton which are detailed below. All sites were cobble bottom streams. Altitude of the sites ranged from 163 to 1061 m asl and average channel width ranged from 1.9 to 30.7 m (Appendix 1).

Physicochemical variables

Depth and water velocity were recorded with a Marsh-McBirney flowmate current meter at five equidistant points along the thalweg. Conductivity, temperature, dissolved oxygen concentration and percent saturation, and pH were measured using a YSI 556 MPS meter. Nitrate, phosphate and ammonia were calculated using a Beckman Coulter DU® Series 700 UV/Vis Scanning Spectrophotometer. Substrate size composition was assessed by sampling 100 stones using the Wolman walk methodology (Wolman 1954). This was converted to a substrate size index following Jowett and Richardson (1990). Substrate heterogeneity was assessed using the Shannon diversity index. Bed stability was assessed using the bottom component of the Pfankuch stability index (Pfankuch 1975). Flow type of each site was assessed visually as percentage of still, backwater, pool, run or riffle over a 100 m reach. Leaf litter percentage, riparian vegetation and % canopy cover were also assessed visually.

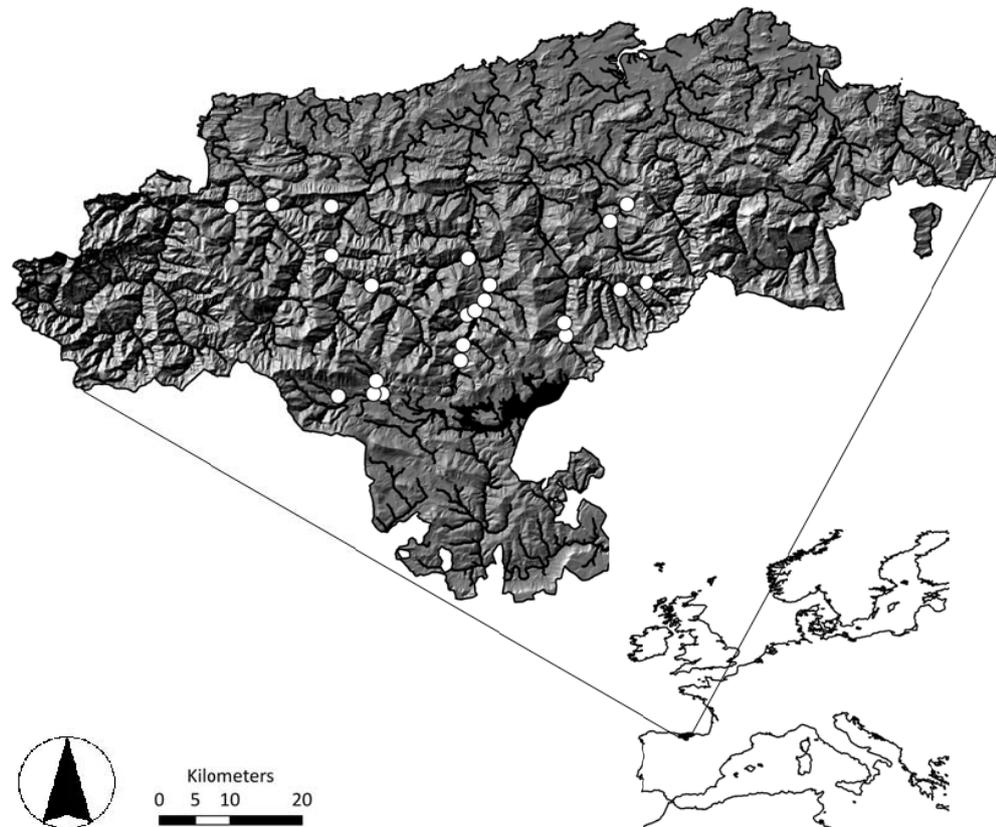


Figure 1: Map showing the location of 24 streams in Cantabria, Spain, sampled in July 2007. Latitudes and longitudes are given in Appendix 1.

Biological collections

Periphyton and primary productivity

Primary productivity was not measured directly but estimated from periphyton biomass (Morin et al. 1999). Biomass was measured by extracting chlorophyll *a* from five stones (mean area: 60 cm²) collected randomly from each site. These were kept cool and dark before being frozen. Chlorophyll *a* and phaeophytin were extracted using 90 % acetone at 5°C for 24 h in the dark. Absorbances were read on a Beckman Coulter DU® Series 700 UV/Vis Scanning Spectrophotometer and converted to pigment concentration following Steinman and Lamberti (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. The relationship between primary productivity and chlorophyll *a* from stones in streams has been found to be strongly related (Morin et al. 1999, Tonkin and Death In prep.). Morin et al. (1999) reviewed

this relationship and found chlorophyll *a* extracted from periphyton and primary productivity were strongly log linearly related ($r^2 = 0.63$). Tonkin et al. (In prep.) also found a strong linear link between chlorophyll *a* biomass accumulation on tiles and chlorophyll *a* content of stones $r^2 = 0.74$). We calculated two other metrics to assess periphyton communities: percent cover of diatoms and mats, and percent cover of filamentous algae. These were assessed visually along three transects across the stream bed using rapid assessment protocols (Biggs and Kilroy 2000). Subsequently, we grouped all algal forms into two groups: periphytic films and mats and filamentous forms. For the sake of simplicity, periphytic mats will be called diatoms although it includes all crustose, prostrate and stalked algae forms.

Macroinvertebrates

Five 0.1 m² 500 µm mesh Surber samples were collected at random from riffles at each site. In the field samples were preserved in 10 % formalin. In the laboratory the samples were washed through 500 µm and 1 mm Endecott sieves before being identified and enumerated to the lowest possible taxonomic level. Invertebrates were mostly identified to morphospecies, however, where possible morphospecies were identified using available keys (e.g. Tachet et al. 2000).

The number of animals per 0.1 m² (density) was calculated for each individual sample and averaged per site as was the number of taxa (richness). Rarefied richness (ES[N]) was calculated in Primer v6 (Clarke and Gorley 2006) for 261 individuals which was the lowest average number of animals at a site. Rarefaction accounts for the passive increase in the number of taxa collected with increasing number of individuals collected (Sanders 1968, Hurlbert 1971). This, in effect, standardises sites by predicting richness per a set number of animals rather than a set area. The final community metric used was the percent of Ephemeroptera, Plecoptera and Trichoptera (EPT) animals per sample (Lenat 1988).

Statistical methods

To test whether diversity, periphyton metrics or other physicochemical variables differed between high and low productivity sites, Analysis of Variance (ANOVA) was

used in Statistix (Statistix 8 ©, Analytical Software, Tallahassee, FL, U.S.A.). We used a randomised complete block (RCB) design using productivity groups as the treatment and catchments as blocks. This method reduces experimental error by dividing into similar groups (i.e. catchment). Analysis of Similarities (ANOSIM) (Clarke 1993) was performed on normalised physicochemical data using Euclidean distances to assess whether site characteristics differed between high and low productivity treatments in Primer v6 (Clarke and Gorley 2006).

To visualise differences in community structure between the two productivity treatments and catchments, 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). Using $\log(x+1)$ transformed data, we used the similarity percentages (SIMPER) (Clarke 1993) procedure in Primer v6 (Clarke and Gorley 2006) to assess which taxa were contributing most to differences in community structure between high and low productivity sites. Regression was also used to examine relationships between primary productivity, percent diatom and filamentous cover and invertebrate metrics, and some physicochemical variables using Statistix (Statistix 8 ©, Analytical Software, Tallahassee, FL, U.S.A.). Where required, data were $\log(x + 1)$ transformed to remove heteroscedasticity.

To analyse which variables best predicted invertebrate and periphyton metrics we used M5 pruned regression trees using Weka 3.6 (Hall et al. 2009). These were re-run using 5-fold cross validation to test whether the model was applicable outside the particular sites used. Classification and Regression Tree (CART) analysis was also run to predict the four measures of periphyton from the remaining physicochemical variables.

Results

Physicochemical characteristics

Conductivity ranged from 68 to 402 $\mu\text{S cm}^{-1}$ (Appendix 1). Conductivity and dissolved oxygen were the only physicochemical variables to differ between high and low productivity sites (Table 1). Conductivity was nearly twice as high on average at high

productivity sites (low mean = 157 $\mu\text{S cm}^{-1}$, high mean = 255 $\mu\text{S cm}^{-1}$) and dissolved oxygen averaged 9.85 mg l^{-1} at low productivity sites compared to 10.44 mg l^{-1} at high productivity sites (Table 1; Appendix 1). The bottom component of the Pfankuch stability index did not differ between low and high productivity sites (Table 1). There was no difference in physicochemical data between productivity treatments with either all variables included ($R = 0.16$, $P = 0.34$) or on the remainder of variables with conductivity and dissolved oxygen removed ($R = -0.05$, $P = 0.85$).

Table 1: Randomised complete block analysis of variance (ANOVA) results for differences in mean physicochemical and biological variables between *a priori* selected productivity groups in 24 streams of Cantabria, Spain, July 2007. Productivity group is the treatment and catchment the block. D.O. = dissolved oxygen, O.H. Cover = overhead cover. Degrees of freedom for the *F*-test for all variable is 1, 17.

	Productivity		<i>F</i>	<i>P</i>
	Low (S.E.)	High (S.E.)		
Pfankuch bottom	31.92 (2.04)	33.58 (2.88)	0.21	0.65
Altitude	393.17 (86.21)	433.17 (77.49)	0.72	0.41
pH	8.81 (0.06)	8.91 (0.07)	1.49	0.24
Conductivity ($\mu\text{S cm}^{-1}$)	156.67 (20.75)	255.25 (24.95)	10.92	0.004
Temperature ($^{\circ}\text{C}$)	15.62 (0.57)	14.69 (0.52)	1.38	0.26
D.O. (mg l^{-1})	9.85 (0.12)	10.44 (0.19)	7.58	0.01
D.O. (%)	98.93 (0.89)	102.03 (2.11)	1.63	0.22
O.H. Cover (%)	35.42 (8.52)	29 (6.93)	0.31	0.59
Velocity (m s^{-1})	0.4 (0.04)	0.39 (0.04)	0.07	0.79
Depth (cm)	19.7 (1.24)	18.02 (1.54)	1.02	0.33
Width (m)	7.39 (1.08)	8.05 (2.29)	0.18	0.68
Substrate size index	147.04 (6.8)	131.17 (9.85)	1.94	0.18
Substrate heterogeneity	1.97 (0.05)	1.99 (0.03)	0.2	0.66
Slope ($\text{m } 100\text{m}^{-1}$)	5.08 (0.94)	5.28 (0.83)	0.02	0.89
Nitrate (mg l^{-1})	0.69 (0.18)	0.93 (0.14)	2.07	0.17
Phosphate (mg l^{-1})	0.43 (0.08)	0.37 (0.04)	0.32	0.58
Ammonia (mg l^{-1})	0.05 (0.01)	0.07 (0.02)	0.87	0.36
Chlorophyll <i>a</i> ($\mu\text{g cm}^{-2}$)	4.47 (0.84)	7.22 (1.05)	3.91	0.07
Diatom (%)	57.22 (7.71)	39.31 (7.49)	4.97	0.04
Filamentous algae (%)	3.56 (1.48)	44.5 (8.77)	18.9	0.0004
Total peri. cover (%)	60.78 (8.38)	83.81 (6.97)	4.9	0.04
Bryophyte (%)	5.5 (4.96)	1.39 (0.96)	0.55	0.47
No. of taxa	16.15 (0.77)	15.05 (0.91)	1.24	0.28
Log (no. of animals)	2.54 (0.05)	2.76 (0.1)	3.25	0.09
ES(261)	15.37 (0.69)	13.48 (0.88)	3.43	0.08
% EPT animals	0.63 (0.05)	0.5 (0.05)	4.19	0.06

Periphyton

Primary productivity, assessed as mean chlorophyll *a*, ranged from 2.58 to 15.35 $\mu\text{g cm}^{-2}$ (Appendix 1). Mean chlorophyll *a* was greater at high productivity sites than low productivity sites but the difference was only significant at the 10 % level (Table 1). Percent diatom cover was lower and filamentous algae cover was more than ten times greater at high productivity sites. Chlorophyll *a* was negatively correlated with percent diatom cover ($r = -0.41$, $P = 0.045$) and positively correlated with filamentous cover ($r = 0.63$, $P = 0.001$), and filamentous cover was negatively associated with diatom cover ($r = -0.5$, $P = 0.013$). Chlorophyll *a* ($F_{1,22} = 15.64$, $P = 0.0007$, $r^2 = 0.416$, $y = 0.81 + 0.02x$) and percent filamentous algae cover ($F_{1,22} = 29.05$, $P < 0.0001$, $r^2 = 0.569$, $y = -26.05 + 0.24x$) increased linearly whereas percent diatom cover declined with increasing conductivity ($F_{1,22} = 5.99$, $P = 0.02$, $r^2 = 0.214$, $y = 76.37 - 0.14x$; Fig. 2).

Community composition

Ordination and ANOSIM on $\log(x + 1)$ transformed invertebrate data indicated community composition did not differ between high and low productivity treatments ($R = 0.05$, $P = 0.16$) or between catchments ($R = 0.002$, $P = 0.47$; Fig. 3). Filamentous algae cover and chlorophyll *a* were positively correlated with MDS 1 ($r = 0.47$ and 0.23 respectively) and negatively correlated with MDS 2 ($r = -0.19$ and -0.28 respectively), whereas diatom cover was negatively correlated with MDS 1 ($r = -0.27$) and positively correlated with MDS 2 ($r = 0.52$).

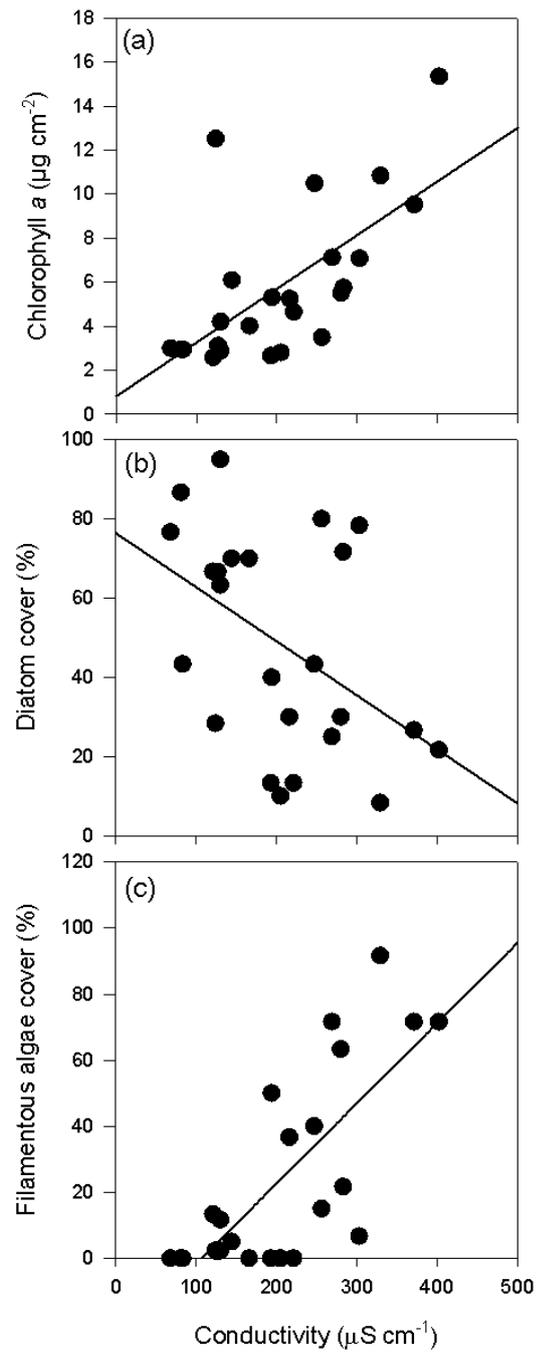


Figure 2: Periphyton metrics as a function of conductivity in 24 streams in Cantabria, Spain, July 2007. (a) Chlorophyll *a*, (b) diatom cover, (c) filamentous algae cover.

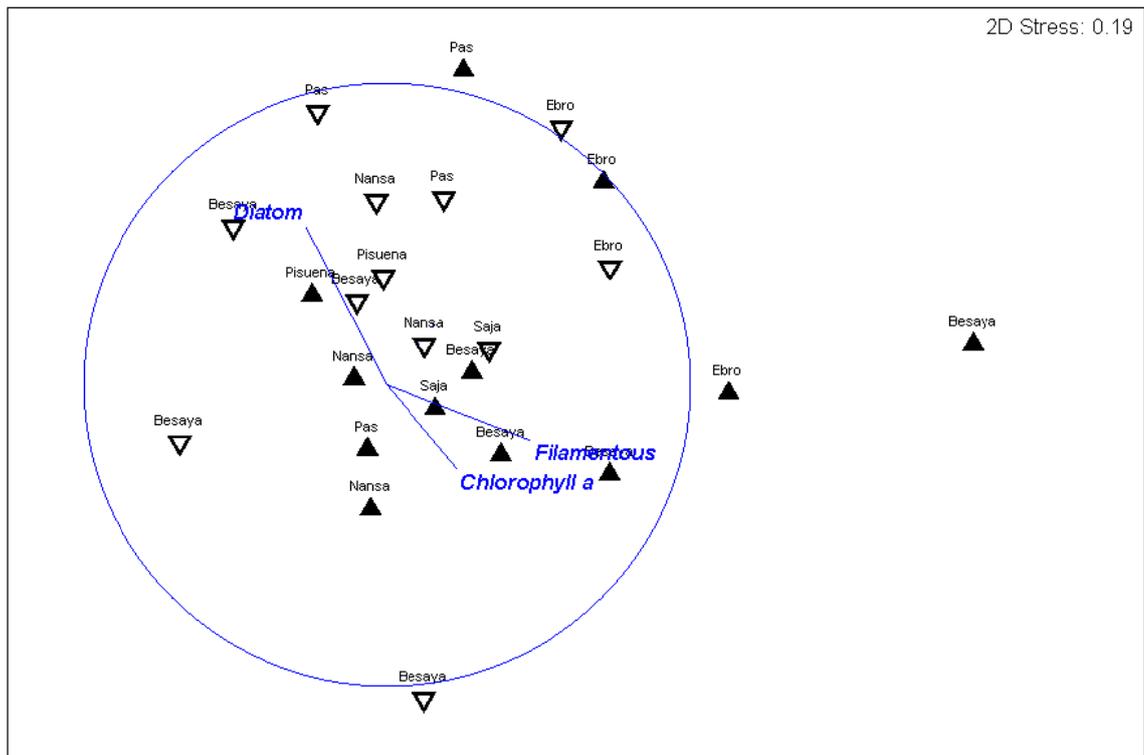


Figure 3: Non-metric multidimensional scaling (NMDS) ordination on $\log(x + 1)$ transformed invertebrate community data collected from 24 streams in Cantabria, Spain, July 2007. Open triangles are *a priori* selected low productivity sites and closed are high productivity. Names above symbols represent the six catchments sites belong to (Besaya, Saja, Pas, Pisueña, Nansa, and Ebro). Results of ANOSIM testing between groups and axis correlations are given in the text. 2D stress = 0.19.

Ten taxa contributed 86 % to the difference in invertebrate community composition ($\log[x+1]$ transformed) between high and low productivity treatments (Table 2). The simuliid *Prosimulium* spp. and mayfly *Baetis* spp. each contributed more than 25 percent to the difference in productivity treatments (Fig. 4; Table 2). However, both density and percent composition of *Prosimulium* spp. (Density: $F_{1,22} = 1.36$, $P = 0.26$; Percent: $F_{1,22} = 3.28$, $P = 0.08$) and *Baetis* spp. (Density: $F_{1,22} = 2.04$, $P = 0.17$; Percent: $F_{1,22} = 0.22$, $P = 0.64$) were not significantly different between high and low productivity sites (Fig. 4). Percent *Prosimulium* spp. was lowest at intermediate levels of diatom cover ($F_{2,21} = 7.39$, $P = 0.004$, $r^2 = 0.41$) and exhibited a quadratic increase with increasing filamentous cover ($F_{2,21} = 2.94$, $P = 0.075$, $r^2 = 0.22$). Percent *Baetis* spp. peaked at intermediate levels of diatom cover ($F_{2,21} = 6.25$, $P = 0.007$, $r^2 = 0.37$). The amphipod *Echinogammarus* spp. contributed over 9 percent to the difference in invertebrate communities between productivity treatments (Fig. 4; Table

2). However, neither density ($F_{1,22} = 2.32$, $P = 0.14$) or relative abundance ($F_{1,22} = 0.76$, $P = 0.39$) were significantly different between productivity treatments. Moreover, percent *Echinogammarus* spp. did not respond to either diatom ($F_{1,22} = 1.49$, $P = 0.24$, $r^2 = 0.06$) or filamentous cover ($F_{1,22} = 1.98$, $P = 0.17$, $r^2 = 0.08$).

Table 2: Differences in community composition between the *a priori* productivity groups in 24 streams sampled in Cantabria, Spain, July 2007. Table shows Similarity percentages (SIMPER) showing the ten taxa contributing to the greatest difference between low and high productivity streams. Av.Abund = average abundance, Av.Diss = average dissimilarity, Diss/SD = standard deviation of dissimilarity, Contrib% = % contribution, Cum.% = cumulative % contribution.

Species	Low P	High P	Av.Diss	Diss/SD	Contrib%	Cum.%
	Av.Abund	Av.Abund				
<i>Prosimulium</i> spp.	50.53	699.78	15.32	0.85	28.11	28.11
<i>Baetis</i> spp.	196.53	365.7	14.01	1.58	25.69	53.8
<i>Echinogammarus</i> spp.	20.77	56.87	5.28	0.85	9.69	63.49
Orthocladiinae b	17.8	119.9	3.13	0.92	5.75	69.23
<i>Ephemerella</i> spp.	22	18.43	2.1	0.93	3.86	73.09
<i>Bythinella</i> spp.	12.52	8.45	1.84	0.66	3.38	76.47
<i>Protonemura</i> spp.	19.87	8.92	1.56	1.09	2.86	79.34
<i>Hydropsyche</i> spp.	20.87	5.53	1.51	0.81	2.78	82.11
Orthocladiinae a	1.82	41.2	0.94	0.7	1.72	83.83
Oligochaeta	4.23	21.75	0.93	0.84	1.71	85.54

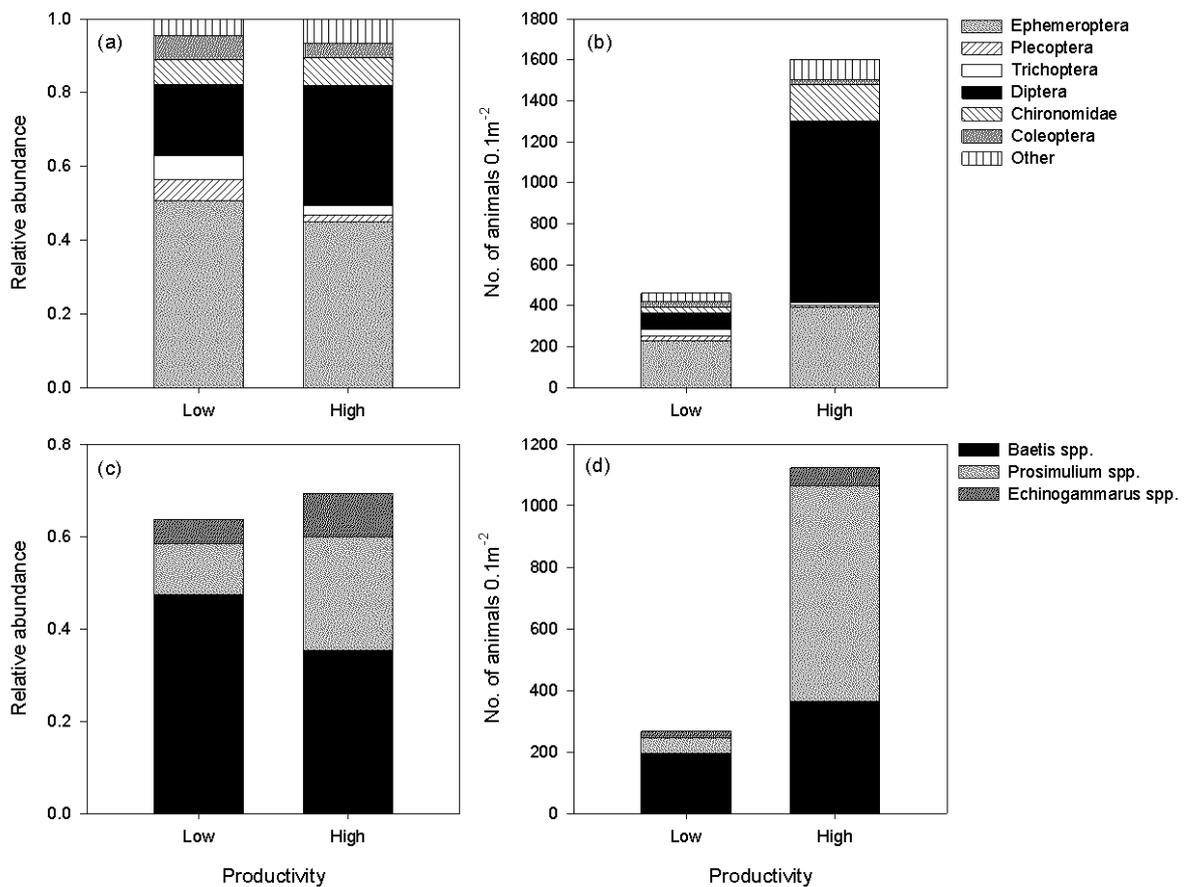


Figure 4: (a) Relative abundance and (b) mean abundance of all taxa between *a priori* selected high and low productivity sites in 24 streams in Cantabria, Spain, July 2007. (c) Relative abundance and (b) mean abundance of the three most dominant taxa between *a priori* selected high and low productivity sites.

Density and diversity patterns

Rarefied richness and % EPT animals were higher and total number of animals lower at low productivity sites, although these differences were only significant at the 10 % level (Table 1). The number of taxa did not differ between high and low productivity sites. The only aspect of the invertebrate community to respond to chlorophyll *a* was the number of individuals which increased monotonically with increasing biomass (Fig. 5; Table 3). Taxonomic richness, rarefied richness and the % EPT animals were not related to chlorophyll *a* (Fig. 5; Table 3).

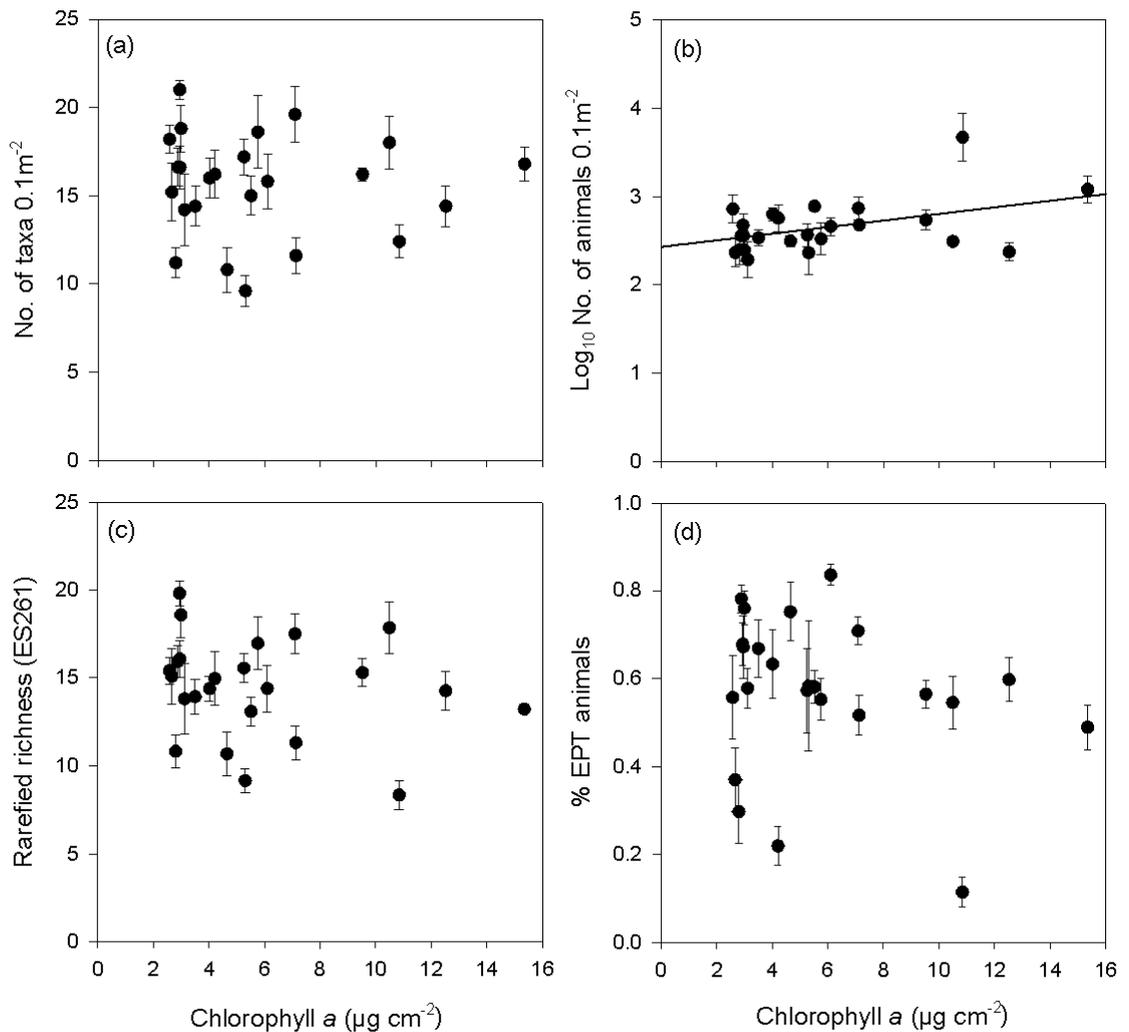


Figure 5: (a) Mean (± 1 S.E.) taxonomic richness, (b) number of animals, (c) rarefied richness, and (d) percent EPT animals as a function of chlorophyll *a* in 24 streams of Cantabria, Spain, July 2007.

Density and diversity measures exhibited opposing responses to the two growth forms of periphyton measured. In general, the response to increasing diatom cover was mainly positive whereas, with the exception of density, the response to increasing filamentous cover was negative. Taxonomic richness and rarefied richness increased log-linearly with increasing substrate cover of diatoms (Fig. 6; Table 3). The number of individuals was not related to percent diatom cover. The percentage of EPT animals appeared more sensitive to higher percentages of diatom cover and peaked strongly at intermediate levels and declined at higher levels of diatom cover. Taxonomic richness was not related to percent filamentous algae cover, however density of individuals exhibited quadratic increase with increasing filamentous cover.

Both rarefied richness and % EPT animals responded negatively to filamentous algae exhibiting a curvilinear decline with increasing filamentous cover.

Table3: Results for regression analysis for taxonomic richness, number of animals, rarefied richness, and percent EPT animals against periphyton metrics for 24 streams in Cantabria, Spain, July 2007. a) Chlorophyll *a*, b) percent diatom cover, and c) percent filamentous algae cover. Degrees of freedom for linear and log-linear models are 1, 22 and for quadratic models are 2, 21. AIC = Akaike's information criterion for the selection of the best model between log-linear and quadratic curves. Lowest values represent the best model.

	<i>F</i> (AIC)	<i>P</i>	<i>r</i> ²	Equation
a) Chlorophyll <i>a</i> (µg cm⁻²)				
No. of taxa	0.05	0.83	0.002	Non-significant
Log (no. of animals)	5.31	0.03	0.194	$y = 2.43 + 0.037x$
ES(261)	0.91	0.35	0.040	Non-significant
% EPT animals	1.14	0.30	0.049	Non-significant
b) Diatom cover (%)				
No. of taxa	9.62 (42.8)	0.01	0.304	$y = 7.55 + 2.2 \ln(x)$
Quadratic	4.91 (43.1)	0.02	0.319	$y = 10.7 + 0.19x - 0.002x^2$
Log (no. of animals)	0.62	0.44	0.027	Non-significant
ES(261)	12.77 (42.3)	0.002	0.367	$y = 5.73 + 2.37 \ln(x)$
Quadratic	6.38 (42.8)	0.007	0.378	$y = 9.08 + 0.21x - 0.0016x^2$
% EPT animals	9.36	0.001	0.471	$y = 0.15 + 0.02x - 0.0002x^2$
c) Filamentous algae cover (%)				
No. of taxa	1.59	0.22	0.067	Non-significant
Log (no. of animals)	13.71	0.0002	0.566	$y = 2.59 - 0.011x + 0.0002x^2$
ES(261)	4.22	0.03	0.287	$y = 14.93 + 0.059x - 0.001x^2$
% EPT animals	4.19	0.03	0.285	$y = 0.58 + 0.006x - 0.0001x^2$

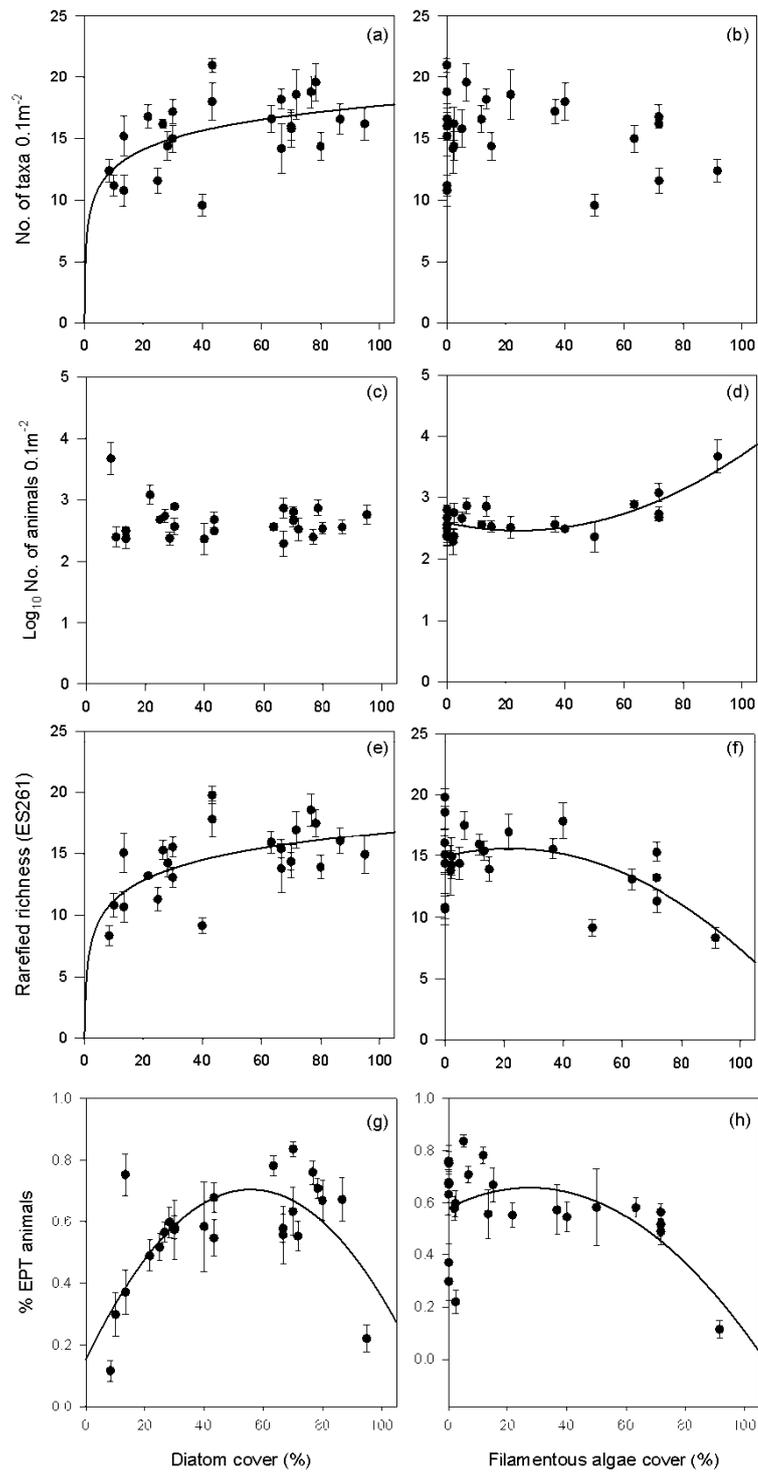


Figure 6: (a, b) Mean (± 1 S.E.) taxonomic richness, (c, d) number of animals, (e, f) rarefied richness, and (g, h) percent EPT animals as a function of percent diatom cover (a, c, e, g), and percent filamentous algae cover (b, d, f, h) in 24 streams of Cantabria, Spain, July 2007.

Classification and regression trees

Regression trees predicted taxa number well (82 % variation explained in full data set and 51 % in cross validation, Table 4). Sites were split into four groups at two levels (Fig. 7; Table 4). As predicted, the type of algae was important in predicting diversity with the initial split grouping sites either side of 42 % diatom cover. High diatom sites (17.2 taxa) had greater diversity than low diatom sites (13.7 taxa) ($F_{1, 22} = 4.3$, $P = 0.001$). The sites with less than 42 % diatom cover (LM1 and LM2) were further split into stable or unstable groups based on the Pfankuch bottom component score of 25 (Fig. 7; Table 4). The low diatom sites were explained by linear model 1 and 2 consisting of the Pfankuch bottom component, percent diatom, altitude, and substrate size (Fig. 7; Table 4). The eight unstable sites (LM2) had the lowest taxonomic richness. The high diatom sites (LM3 and LM4) were further split based on phosphate levels and were predicted by chlorophyll *a*, diatom cover and altitude. The high phosphate group (LM4), which included 7 sites, had 15.9 taxa per site.

The remaining measures of density and diversity related to measured environmental variables in a more straightforward single linear model. The number of animals was best predicted by altitude and conductivity (Table 4). Rarefied richness was predicted by diatom cover (53 % variation explained in full set and 29 % in cross validation; Table 4). None of the measured variables could predict % EPT animals (Table 4).

Conductivity was the best predictor of primary productivity and periphyton cover and was included in the prediction models of all three periphyton metrics (Table 4). Division of sites was not required for the prediction of these metrics. Chlorophyll *a* was predicted well by pH, conductivity and velocity (83 % variation explained in full set and 56 % in cross validation; Table 4). Diatom cover was predicted by conductivity and temperature (62 % variation explained in full set and 29 % in cross validation; Table 4). Conductivity predicted filamentous algae cover percentage (75 % variation explained in full set and 60 % in cross validation; Table 4).

Table 4: Fit statistics showing the results of M5 pruned classification and regression tree (CART) analysis predicting invertebrate community metrics and four measures of periphyton in 24 streams in Cantabria, Spain, July 2007. S = number of taxa, LogN = log (number of animals), ES(261) = rarefied richness for 261 individuals, LM = linear model, RMSE = root mean square error, RRSE = root relative square error.

(a)	Training data			5-fold cross validation		
	Correlation coefficient	RMSE	RRSE	Correlation coefficient	RMSE	RRSE
S	0.815	1.71	60.3	0.51	2.45	85.13
LogN	0.6	0.23	80	0.078	0.34	112.78
ES(261)	0.529	2.37	84.84	0.289	2.85	100.64
% EPT animals	0	0.17	100	-0.319	0.27	147.75
Chlorophyll <i>a</i>	0.83	1.92	55.85	0.559	2.96	84.78
Diatom	0.615	21.08	78.83	0.294	27.76	99.55
Filamentous	0.754	19.19	65.64	0.602	24.46	81.94

(b)	Model	Equation
S	LM1	$S = -0.07(\text{Pfankuch}) + 0.03(\text{Diatom}) + 0.002(\text{Alt.}) + 4.57(\text{Substrate}) + 5.63$
	LM2	$S = -0.06(\text{Pfankuch}) + 0.03(\text{Diatom}) + 0.0008(\text{Alt.}) + 5.42(\text{Substrate}) + 3.42$
	LM3	$S = 0.17(\text{Chlorophyll } a) + 0.03(\text{Diatom}) + 0.003(\text{Alt.}) + 12.94$
	LM4	$S = 0.17(\text{Chlorophyll } a) + 0.03(\text{Diatom}) + 0.003(\text{Alt.}) + 12.60$
LogN	LM1	$\text{LogN} = 0.0004(\text{Alt.}) + 0.002(\text{Cond.}) + 2.112$
Rarefaction	LM1	$\text{ES}_{261} = 0.06(\text{Diatom}) + 11.75$
% EPT animals	LM1	$\% \text{ EPT animals} = 0.57$
Chlorophyll <i>a</i>	LM1	$\text{Chlorophyll } a = 5.82(\text{pH}) + 0.02(\text{Cond.}) - 11.04(\text{Velocity}) - 45.14$
Diatom	LM1	$\text{Diatom} = -0.11(\text{Cond.}) + 5.98(\text{Temp.}) - 20.17$
Filamentous	LM1	$\text{Filamentous} = 0.24(\text{Cond.}) - 26.05$

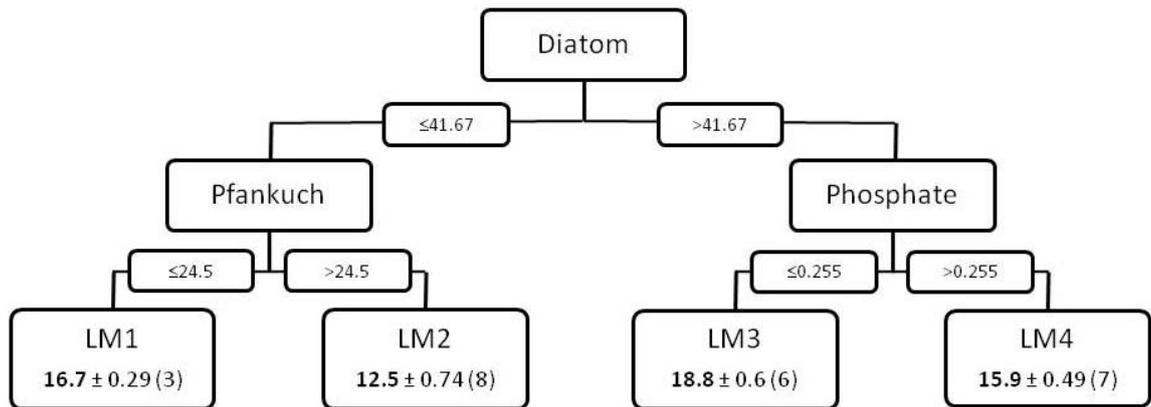


Figure 7: M5 pruned regression tree generated for the prediction of the number of taxa in 24 streams of Cantabria, Spain, July 2007. The tree shows the relationship between three explanatory variables and the levels at which the splits occur. Mean (± 1 S.E.) number of taxa per site are given in each terminal node with the number of sites predicted for each node given in parentheses. Diatom = % diatom cover, Pfankuch = bottom component of the Pfankuch stability index, Nitrogen = mg L^{-1} . LM1 – LM4 = linear model 1 - 4. See Table 4a for fit statistics and 4b for equations for each linear model.

Discussion

There was no relationship between periphyton biomass and invertebrate diversity in this study. This suggests there was no clear relationship between primary productivity and invertebrate diversity as primary productivity and benthic periphyton biomass is strongly linked in streams (Morin et al. 1999, Tonkin and Death In prep.). Meta analyses have shown that approximately one third of all studies looking at the productivity-diversity relationship find no significant link between the two, but this can vary with spatial scale, community type and between plants and animals (Waide et al. 1999, Mittelbach et al. 2001). It appears that this lack of relationship between productivity and diversity is more common at smaller scales, such as this study, with links between the two more commonly found at larger spatial scales (Mittelbach et al. 2001). We must interpret this data with caution as there is now considerable debate about the robustness of the meta-analyses used to collate data addressing this question (Hillebrand and Cardinale 2010, Whittaker 2010). Recently, several studies in stream communities have found log-linear increases in diversity with productivity (Death 2002, Barquin 2004, Tonkin and Death In prep., Tonkin et al. In prep.). This,

and the belief that increased productivity does not lead to greater rates of competitive exclusion in streams, led us to predict this log-linear trend would occur in these Spanish streams; however this was not the case. Lamberti et al. (1989) suggest changes in herbivore biomass may better represent the production of stream communities (i.e. primary productivity) than algal biomass due to the strong role of herbivory suppressing algal biomass in streams, although this does not account for disturbance.

Although invertebrate communities did not respond clearly to changes in primary productivity, the form of the periphyton community was important in determining diversity patterns. There has been extensive research on the effects of grazers on algal communities, but other than grazer specific responses (e.g. Gresens and Lowe 1994, Maasri et al. 2008), the reverse effects of algal assemblages on invertebrate communities has received little direct attention in streams (but see Dudley et al. 1986, Koksvik and Reinertsen 2008). However, it is clear that the type of periphyton has strong influences on the structure of stream benthic communities (Dudley et al. 1986, Koksvik and Reinertsen 2008), and grazing communities can in fact grow at different rates depending on the form of algae present (Feminella and Resh 1991). In the present study, there were clear opposing influences of the two main growth forms measured, with general patterns suggesting diatom cover generated a positive response, and filamentous cover a negative response, of invertebrate communities. However, invertebrate community composition did not vary strongly between high and low productivity streams. Differences were mainly due to changes in the densities of the three dominant taxa: the blackfly larvae *Prosimulium* spp., the mayfly *Baetis* spp. and amphipod *Echinogammarus* spp.. Barquin and Death (2004) also found these taxa in high densities in streams of this region.

Percent diatom cover was the best predictor of diversity with both taxonomic and rarefied richness increasing log-linearly as cover increased. This mirrors the hypothesis we set of a log-linear curve for the relationship between primary productivity and diversity that several recent studies have found in benthic communities (Death 2002, Barquin 2004, Tonkin and Death In prep., Tonkin et al. In prep.). Diatom forms of algae are the most important food source for a high

proportion of benthic invertebrates as grazers tend to be able to assimilate diatoms better than other algal growth forms (Lamberti et al. 1989).

The percent of EPT animals responded negatively at the highest levels of diatom cover. These taxa are considered sensitive to “pollution”, thus the response found here may indicate that higher levels of diatom cover are associated with nutrient enrichment. However, the response of % EPT at high diatom cover is largely due to one dominant taxon – *Baetis* spp. – which was one of the most abundant taxa in all streams. The decline at higher diatom levels may be due to the fact that more palatable forms of diatoms become shaded out by prostrate forms when growth becomes more prolific. *Baetis* often use diatoms as a food source and their prevalence can vary greatly with types of algae depending on the stage in their lifecycle (Dudley et al. 1986). Mayflies generally tend to favour grazing diatoms (Jacoby 1987) and due to the large proportion of grazers, EPT taxa often respond negatively to filamentous algae (Quinn and Hickey 1990, Suren 2005). Consequently, we expected a strong decline in % EPT with filamentous cover but it remained relatively high up to three quarters of bed cover of filamentous algae. Filamentous algae may provide a greater retention of organic detrital material that in turn would support more shredding taxa. However the shredder/predator *Echinogammarus* spp. did not respond to either form of periphyton. Barquin and Death (2004) found *Echinogammarus* to be dominant in spring-fed streams in Cantabria and suggested this may be a consequence of increased biotic interactions associated with environmental stability (Connell 1978), thus causing suppression of other invertebrates. We found no evidence to suggest lower diversity at sites with greater densities of *Echinogammarus*.

The number of animals increased rapidly with filamentous cover largely as a result of *Prosimulium* spp. becoming dominant. The response of *Prosimulium* to increased filamentous cover is variable due to their life histories (Townsend 1981, Dudley et al. 1986, Morin and Peters 1988); black flies (Simuliidae) are often associated with bare substrates but smaller individuals are often found in high densities attached to filamentous algae (Dudley et al. 1986). Black fly larvae are filter feeders capturing their food from drifting organic seston and so do not directly browse upon periphyton, but can be found in high densities in enriched rivers feeding upon drifting algal cells

(Peterson et al. 1985) as do other filter-feeding invertebrates (Benke and Wallace 1980, Wallace and Merritt 1980).

The number of taxa inhabiting substrates did not change with increasing filamentous algae cover. However, due to marked increases in *Prosimulium* spp., rarefied richness declined strongly at intermediate levels. When levels of periphyton reach greater densities and epilithic diatoms are replaced by macroalgae such as filamentous green algae, more complex relationships tend to develop involving habitat provision and exclusion as well as direct food interactions (Dudley et al. 1986). Dense layers of filamentous algae can lead to the displacement of sensitive taxa by those that can tolerate large diurnal fluctuations in dissolved oxygen. For example, chironomids are often associated with macroalgae whereas EPT taxa are not (Power 1990, Koksvik and Reinertsen 2008, Maasri et al. 2008). Although we have coarsely classed growth forms into two broad categories, benthic invertebrates often have specialist feeding traits for these two algal forms. Steinman et al. (1992) found the snail *Elimia* avoided both gelatinous and unbranched filamentous growth forms and favoured diatoms; they suggest this may be due to a lack of ability to digest filamentous forms. It has also been suggested that stream herbivores typically reject filamentous algae when selecting food sources (Gregory 1983), possibly because they often have high cellulose content and thick walls (Lamberti and Moore 1984). This selectivity goes beyond the coarse levels assessed here. For example, Hambrook and Sheath (1987) show that selective grazing can come within filamentous forms where preferences were shown for simple unbranched rhodophytes over branched and mucilaginous.

The dense levels of filamentous algae found here is potentially a result of such selective grazing which can alter plant communities by reducing palatable forms and leaving non-palatable forms behind (Sousa 1984, Wardle et al. 2001, Brathen et al. 2007). The dominant invertebrate taxa found in this study are not typically associated with grazing filamentous algae, although as previously stated, simuliids can be found filter feeding on drifting algal cells but this does not suppress growth. Grazers can alter periphyton community structure within and between micro and macro algal forms in lotic systems (Lamberti and Resh 1983, McAuliffe 1984, Dudley et al. 1986, Feminella and Resh 1991), and the suppression of palatable forms can lead to

communities consisting of resistant prostrate blue-green algae (Hart 1985, Power et al. 1988). In fact, selectivity is often so strong that grazing insects may remove, without ingesting, unfavourable forms in order to allow favourable forms to remain for grazing (Hart 1985).

Management implications

Many relationships in nature are nonlinear (Dodds et al. 2010), thus we must consider this when interpreting results such as those found here. Nonlinearity has recently been recognised for the setting of ecological thresholds of anthropogenic impact (Hilderbrand et al. 2010) and assessing recovery from stressors (Clements et al. 2010) in lotic systems. Odum et al. (1979) introduced the concept of a subsidy-stress effect to demonstrate the response of biotic communities to environmental perturbations such as increased nutrients. In some cases an ecosystem may initially respond positively to a perturbation, such as increased nutrients, before becoming stressed at greater levels. Although shifts in the form of periphyton cover is not an environmental perturbation *per se*, if we consider this within a subsidy-stress framework (i.e. the environmental gradient as the percent cover of periphyton forms and the biological response as invertebrate community metrics), increased diatom cover generally appears to be a subsidy and increased filamentous cover a stressor. This subsidy-stress effect is common in natural systems (Odum et al. 1979, Megonigal et al. 1997, King and Richardson 2007) and can occur in lotic systems as a result of land-use change altering levels of nutrients, available light and sediment (Quinn 2000, Niyogi et al. 2007). It is likely that the real perturbation leading to these subsidy-stress effects in these streams is increasing nutrient levels. Long term increases in nutrients can lead to the proliferations of filamentous algae similar to those found here. Therefore, growth forms of periphyton are most likely reflecting long-term nutrient levels and leading to individual subsidy and stress effects on diversity.

The need for thresholds in the management of lotic systems (Clements et al. 2010, Dodds et al. 2010, Hilderbrand et al. 2010), leads us to suggest filamentous algal cover would be a useful threshold indicator. Approximately 40 % filamentous cover led to a decline in diversity (richness and rarefied richness) whereas EPT taxa remained

relatively constant up to approximately 75 % cover. Welch et al. (1988) found levels greater than 20 % filamentous algae cover were considered nuisance levels.

The fact that diversity responded more strongly to the form of periphyton than chlorophyll *a* implies this could be a more useful tool for managers interested in preserving biodiversity. Typically, biomonitoring involves assessing periphyton biomass using either chlorophyll *a* and/or ash-free dry weight (AFDW). Although they are often highly correlated, they do not always respond in the same way to environmental conditions (Biggs and Hickey 1994, Feminella and Hawkins 1995, Jowett and Biggs 1997), and they can have very different chlorophyll *a*:carbon ratios (Biggs 2000). Rather than simply measuring chlorophyll *a* or AFDW of periphyton communities, it may be more appropriate to assess the relative abundance of the different growth forms of periphyton. Many have used components of the periphyton community as an index for biomonitoring environmental conditions (Kelly and Whitton 1995, Pan et al. 1996, Kelly 1998b, a, Kelly and Whitton 1998, Hill et al. 2000), however most of these use diatoms exclusively and require large investments in time and money to complete. We have found that periphyton community composition does not need to be measured to a low taxonomic level, and rapid assessment protocols have been developed for this assessment (Biggs and Kilroy 2000). Often the distinction between communities with shifts in relative abundance of filamentous algae and diatoms is obvious. Suren et al. (2003) found invertebrate communities changed from insect to non-insect dominated with shifts in the periphyton community from diatom to filamentous algae dominated.

Conclusions

Our research found no relationship between a commonly used surrogate of productivity (chlorophyll *a*) and diversity in these streams. This is a common finding when exploring productivity-diversity relationships at smaller spatial scales (Waide et al. 1999, Mittelbach et al. 2001). As hypothesized, this relationship was underpinned by contrasting responses of invertebrate communities to the form of the periphyton community. General patterns suggest that diversity responds positively to increasing diatom cover, however sensitive EPT taxa decline at intermediate levels. Conversely,

invertebrate communities responded negatively to increasing filamentous algae cover. This underlying response to the form of periphyton community provides some explanation for the lack of a clear relationship between productivity and diversity in lotic systems. Additionally, our findings have important management implications which demonstrate that the rapid assessment of periphyton growth form can be highly relevant to higher trophic levels. We suggest a threshold of 40 % filamentous cover could be set for managers wishing to minimise deleterious effects of eutrophication on associated invertebrate communities.

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Appendix 1: Mean physicochemical variables and site characteristics recorded at 24 streams in the Cantabrian Mountains, Spain, in July 2007. Alt. = altitude, Pfanck. Bottom = the bottom component of the Pfanck stability index, Cond. = conductivity, Temp. = temperature.

Site	Name	Catchment	Longitude	Latitude	Alt.	Width (m)	Depth (cm)	Velocity (m/s)	Substrate size index	Pfanck. bottom	pH	Cond. (µs/cm)	Temp. (°C)
1	Rio Besaya @ Helguera	Besaya	-4.03276	43.158628	214	10.34	27	0.49	123.07	23	9.3	371	15.49
2	Rio Eracia @ Helguera	Besaya	-4.030378	43.159622	222	7.60	23	0.36	141.54	29	9.03	166	15.91
3	Rio Bisuena @ Barcena Pie de Concha	Besaya	-4.06826	43.121292	309	4.31	26	0.56	131.88	39	8.7	269	14.7
4	Torina @ Barcena Pie de Concha	Besaya	-4.054722	43.126793	299	7.30	22.8	0.20	142.69	27	9.19	124	14.96
5	Santiurde @ Santiurde	Besaya	-4.078611	43.063231	634	4.45	15.2	0.48	127.15	44	8.99	221	12.73
6	Rumadero @ Pesquera	Besaya	-4.074784	43.083177	574	2.10	12.6	0.19	132.02	41	8.84	329	13.77
7	Rio Leon @ San Martin de Quevedo	Besaya	-4.038779	43.139996	264	5.13	18	0.35	142.14	43	8.76	193	16
8	Ayo Valdeiguna @ Pedredo	Besaya	-4.067773	43.192911	185	6.13	16.4	0.23	152.16	26	8.65	205	16.55
9	Rio Argoza @ Barcena Mayor	Saja	-4.232753	43.156963	422	17.50	30.2	0.63	178.53	27	9.02	127	15.2
10	Rio Saja @ Renedo	Saja	-4.30455	43.194076	293	30.70	23.4	0.56	145.22	42	8.97	130	17.79
11	Rio de la Magdalena @ San Andres	Pas	-3.897027	43.096378	412	9.63	23.2	0.31	166.81	30	9.04	194	12.77
12	Ayo Salcera @ San Miguel de Luena	Pas	-3.899921	43.112736	347	2.67	13.4	0.46	158.08	19	8.85	216	12.94
13	Rio Viaña @ Viaña	Pas	-3.804674	43.155633	326	6.97	19.4	0.47	139.45	24	8.66	81	18.63
14	Rio Pas @ Pandillo	Pas	-3.759107	43.164859	366	9.50	20.6	0.54	192.32	30	8.77	130	18.36
15	Llerana @ Coterillo	Pisuena	-3.794589	43.263832	207	5.37	18.4	0.38	137.48	32	8.44	256	15.38
16	Rio Pisuena @ Barcena de Carriedo	Pisuena	-3.823485	43.241998	181	7.33	17.2	0.39	102.32	45	8.48	283	16.82
17	Nansa @ Puentenansa	Nansa	-4.406832	43.257111	168	9.47	20.8	0.36	121.21	41	8.75	303	15.41
18	Ayo de Hoyamala @ Puentenansa	Nansa	-4.406179	43.257101	163	6.15	16.8	0.33	110.22	33	8.59	280	14.02
19	Lamasón @ Quintanilla	Nansa	-4.476253	43.25448	238	6.40	17	0.35	112.50	44	8.78	144	16.42
20	Ayo de Traveseras @ Quitanilla	Nansa	-4.30588	43.256427	239	4.00	13.6	0.22	196.25	24	8.76	247	15.13
21	Palomba @ Paracuelles	Ebro	-4.211634	43.019856	895	1.93	14.4	0.24	61.12	20	9.24	402	12.99
22	Rio Hajar @ Espanilla	Ebro	-4.226527	43.019571	937	13.00	13.4	0.45	119.91	43	9.15	121	17.17
23	Rio Rucebos @ Soto	Ebro	-4.222249	43.035916	960	5.00	14.6	0.52	131.04	34	9.06	68	13.01
24	Rio Guares @ Abiado	Ebro	-4.289066	43.016011	1061	2.27	15.2	0.47	173.46	26	8.63	83	11.55

Chapter 5

Global patterns in stream diversity – productivity relationships



Abstract

More productive environments typically have more species, although the specific form of this relationship is unclear and varies with spatial scale. This relationship has received little direct attention in lotic systems and thus there is no clear understanding of the form of the trend. To examine this relationship in lotic systems and whether a universal trend exists, we examined and compared 24 streams of Cantabria, Spain and 24 of the central North Island, New Zealand between February and July 2007. Based on the notion that productivity dictates the upper limit to richness in streams rather than to increase the effect of competitive interactions, we predicted a log-linear relationship in both regions. Productivity, assessed as chlorophyll *a*, was approximately three times higher in Spanish streams but taxonomic richness of invertebrates did not differ between the two regions. Taxonomic richness (and Shannon diversity) only responded to productivity in the New Zealand streams, exhibiting the predicted log-linear increase. In fact, the only metric to respond to productivity in the Spanish streams was the number of animals which increased monotonically. However, this relationship was assessed at different scales of productivity between the two regions. When fit to the same axis, richness in the Spanish streams was simply a continuation of the log-linear curve fit to the New Zealand streams. With the large range of productivity assessed and no evidence of a decline in diversity with higher productivity, it appears that the view of productivity setting maximum richness, rather than leading to stronger competitive interactions, may be global phenomenon in streams.

Introduction

Predicting diversity remains a fundamental challenge in community ecology (e.g. Huston 1994, Hubbell 2001, Ricklefs 2004). Global patterns suggest diversity is a function of a few broad-scale factors such as latitude, precipitation, temperature, altitude and land mass (Gaston 2000). Of the multitude of factors that can influence diversity (Palmer 1994, Vinson and Hawkins 1998), disturbance (Connell 1978, Wootton 1998, Lake 2000) and productivity (Currie 1991, Waide et al. 1999, Mittelbach et al. 2001) prevail, although universal patterns remain elusive (Waide et al. 1999, Mackey and Currie 2001, Mittelbach et al. 2001). What is likely is disturbance and productivity interact to affect diversity but the nature of this interaction remains unclear (Sousa 1984, Pickett and White 1985, Currie 1991, Wootton 1998, Waide et al. 1999, Mittelbach et al. 2001, Death and Zimmermann 2005, Cardinale et al. 2006).

Few systems are more heavily influenced by disturbance than streams (Resh et al. 1988, Lake 2000, Death 2008), but the response of diversity to disturbance is likely to be dependent on productivity (Death 2002, Cardinale et al. 2005, Death and Zimmermann 2005, Cardinale et al. 2006). Several empirical studies have found an interaction between productivity and disturbance to be important in controlling diversity (e.g. Wilson and Tilman 2002, Kneitel and Chase 2004, Death and Zimmermann 2005, Scholes et al. 2005). However, due to the highly mobile nature of stream invertebrates, successful applications of common models such as the Intermediate Disturbance Hypothesis (IDH) (Grime 1973b, Connell 1978, Sousa 1979) and the Dynamic Equilibrium Model (DEM) (Huston 1979, 1994, Kondoh 2001) are rare (but see Townsend et al. 1997). What makes streams especially unique is the strong association between disturbance and productivity (Lake 2000, Death 2002, Tonkin and Death In prep.-a, Tonkin et al. In prep.-b). Furthermore, there is little evidence in streams of a competition-colonisation trade-off (Reice 1985, Death and Winterbourn 1995). Death (2002) proposed a model suggesting disturbance simply resets the colonization process and productivity, rather than competitive interactions, sets the upper limit to richness in streams. However, whether a great enough range of productivity was sampled to elucidate the full pattern is unclear as this was only

assessed in New Zealand forest streams. In order to understand this interaction between productivity and disturbance in depth, clarification of the productivity-diversity relationship in streams is required.

The two most common forms of the productivity-diversity relationship in all systems are unimodal (e.g. Grime 1973a, Huston 1979, Rosenzweig 1992, 1995, Leibold 1999, Waide et al. 1999, Mittelbach et al. 2001) and linear (e.g. Currie and Paquin 1987, Currie 1991, Abrams 1995, Waide et al. 1999, Gaston 2000, Mittelbach et al. 2001) increases in diversity with increasing productivity. One of the major influences on the form of this relationship is the spatial scale of investigation (Currie 1991, Chase and Leibold 2002, Tonkin and Death In Prep.-b) and the type of ecosystem and/or organisms considered (Waide et al. 1999, Mittelbach et al. 2001). Smaller scale studies commonly find unimodal relationships between productivity and diversity but at greater spatial scales, this pattern often exhibits monotonic increases in diversity with productivity (Waide et al. 1999, Mittelbach et al. 2001, Chase and Leibold 2002). There are many mechanisms postulated to lead to this unimodal relationship (Rosenzweig and Abramsky 1993, Abrams 1995, Waide et al. 1999), but these often require some form of competitive trade-off. However, little effort has been placed on elucidating this relationship in lotic systems. The few to look specifically have found both unimodal (Death and Zimmermann 2005, Cardinale et al. 2006) and log-linear (Death 2002, Barquin 2004, Tonkin and Death In prep.-a, Tonkin et al. In prep.-b) increases in diversity with increasing productivity.

Not only are the effects of productivity dependent on scale, but regional effects such as the potential pool of colonizers can completely alter the response to environmental factors. Two studies by Barquin and Death (2004, 2006) found contrasting responses of invertebrates to environmental stability between Spanish and New Zealand streams. Thus we set out to (i) examine whether the response of stream invertebrate diversity to productivity differs between these two regions at similar distances from the equator in the Northern and Southern Hemispheres; and (ii) whether a universal relationship exists for the productivity-diversity relationship by combining both regions and re-examining the nature of the link. We hypothesise that diversity will be higher in the Spanish streams as they occur within a large continent

with a greater potential pool of colonists. However, we expect that the response of diversity to productivity will be similar between the two regions despite the different taxonomic composition. That is, we hypothesise that diversity will increase with increasing productivity up to a point before tapering off. We also assess whether the percent of Ephemeroptera, Plecoptera and Trichoptera (% EPT) respond differently than typical diversity measures as these taxa are sensitive to ‘pollution’, and associated algal proliferations, in lotic systems. Finally, due to the strong link between productivity and disturbance in streams, we explore the relationship between stability and diversity in these streams and expect that this may explain any lack of pattern with productivity. By combining and comparing two regions at opposing sides of the planet we can potentially provide some clarity to global patterns in the productivity-diversity relationship of lotic systems.

Methods

Study sites

Twenty four streams were sampled in each of the Cantabrian Mountains of Northern Spain and Tongariro National Park in the central North Island of New Zealand between February and July 2007 (Appendix 1). The Cantabrian Mountains span approx. 483 km east to west along the northern coast of Spain reaching 2,648 m asl at Torre de Ceredo. Average rainfall ranges from approx. 1,200 to 1,600 mm p.a. depending on location within the region. Land-use surrounding sampling sites varied from Atlantic deciduous forest consisting predominantly of oak (*Quercus* spp.) and European beech (*Fagus* spp.) to pasture and small urban settlements. Sites were selected from six river catchments: Rio Besaya, Rio Saja, Rio Pas, Rio Pisueña, Rio Nansa, and Rio Ebro. Except for Rio Ebro, which drains into the Mediterranean Sea, all rivers flow into the Atlantic. Altitude ranged from 163 to 1061 m asl and average channel width ranged from 1.9 to 30.7 m.

The Tongariro National 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. The Kaimanawa Ranges rise to ~1,799 m asl to the east of the Tongariro National Park 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. The north and west has an average rainfall of 1,800-3,500 mm yr⁻¹ with the south and east only receiving around 1,100 mm yr⁻¹ due to the rain-shadow cast by the three mountains from the prevailing westerly winds. Sites ranged from 518 to 1158 m asl and average width of stream channels ranged from 1.4 to 30 m.

Sampling protocol

Macroinvertebrates

Macroinvertebrates were sampled by taking five 0.1 m² Surber samples (250 µm mesh in New Zealand samples and 500 µm in Spanish samples) from random locations in riffles throughout ~50 m reaches at each site. Samples were stored in 10 % formalin and later sieved to 500 µm and identified in the laboratory to the lowest possible taxonomic level. New Zealand samples were identified using available keys (e.g. Towns and Peters 1996, Winterbourn et al. 2000) and Spanish samples were mostly identified to morphospecies, however, where possible these were identified using available keys (e.g. Tachet et al. 2000). Four simple measures of diversity were used in this study: number of individuals, number of taxa (richness), Shannon diversity index (H'), and the percent of Ephemeroptera, Plecoptera, Trichoptera (% EPT animals) (Lenat 1988).

Periphyton

Productivity was not directly measured but was estimated from measures of chlorophyll *a* from stream substrata. Chlorophyll *a* and primary productivity in streams are highly correlated (Morin et al. 1999). Tonkin and Death (In prep.-a) found a strong linear link between chlorophyll *a* biomass accumulation on tiles and chlorophyll *a* content of stones ($r^2 = 0.74$).

Five stones (α axis < 60 mm) were randomly collected from each riffle for later extraction of chlorophyll a . From here stones and tiles were kept cool and dark on ice before being stored at -20°C . Photosynthetic pigments were extracted from stones by submerging each stone 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) for New Zealand samples and on a Beckman Coulter DU[®] Series 700 UV/Vis Scanning Spectrophotometer (Beckman Coulter Inc., Brea, CA, USA) for Spanish samples and converted to chlorophyll a and phaeophytin pigment concentration using Steinman and Lamberti (1996). These were then corrected for stone surface area and halved to account for just the active growing area of the stone using Graham et al. (1988).

Other environmental measures

Substrate size composition was assessed using the 'Wolman Walk' method where the β 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 (Quinn and Hickey 1990). Conductivity, temperature and pH were measured using Eutech instruments ECScan pocket meter at New Zealand sites and a YSI 556 MPS meter at Spanish sites. 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. Leaf litter percentage, riparian vegetation and percent canopy cover were also assessed visually.

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, which assesses the substrate component of the stream only, as

this is more relevant to stream invertebrate communities (Winterbourn and Collier 1987, Death and Winterbourn 1994).

Statistical analysis

Principal Component Analysis (PCA) was carried out on normalised environmental data to determine whether physicochemical and habitat variable differed between New Zealand and Spanish streams using Primer v6 (Clarke and Gorley 2006). Differences in principal components between regions were tested for using one-way Analysis of Variance (ANOVA) in Statistix (Statistix 8 ©, Analytical Software, Tallahassee, FL, U.S.A.). Further assessment of whether site characteristics differed between regions was assessed using Analysis of Similarities (ANOSIM) (Clarke 1993) on normalised physicochemical data using Euclidean distances in Primer v6 (Clarke and Gorley 2006). One-way ANOVA was performed on individual physicochemical and biological data to determine whether there were differences in these metrics between Spanish and New Zealand streams using Statistix (Statistix 8 ©, Analytical Software, Tallahassee, FL, U.S.A.).

Where required, data were $\log(x + 1)$ transformed in order to normalise the data. In order to test whether diversity was a log-linear function of productivity as hypothesised, regression analysis was carried out to explore relationships between diversity and chlorophyll *a* within each region as well as combining both regions and testing for a universal relationship using Statistix. Finally, to explore whether stability was important at determining diversity patterns in these streams regression was performed between the Pfankuch index and invertebrate metrics using Statistix, and a second term was added if it yielded a better fit. Akaike's Information Criterion (Akaike 1974) was used to determine the best fitting curve to the data. 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.

Results

Physicochemical variables

Stream habitat and physicochemical conditions were different between New Zealand and Spanish streams (Fig. 1; Table 1). Principle component (PC) 1 (35.6 % variation explained) strongly split New Zealand and Spanish sites based on physicochemical data, but there was no difference between regions on PC2 (16.4 % variation explained) (Fig. 1; Table 1). ANOSIM confirmed there were strong differences in physicochemical variables between the two regions ($R = 0.53$, $P = 0.001$). Conductivity ranged from 44 to 298 $\mu\text{S cm}^{-1}$ in New Zealand and 68 to 402 $\mu\text{S cm}^{-1}$ in Spanish streams and was on average one third higher in the Spanish streams (Table 1). New Zealand streams were more acidic, wider, deeper, and had twice the velocity (Fig. 1; Table 1). There was little or no difference in slope, substrate size index or substrate heterogeneity between the two regions. Bed stability, assessed as the bottom component of the Pfanckuch index, did not differ between New Zealand and Spain (Table 1).

Productivity

Mean chlorophyll a ranged from 2.58 to 15.35 $\mu\text{g cm}^{-2}$ in the Spanish streams and averaged 5.84 $\mu\text{g cm}^{-2}$. Chlorophyll a was on average three times lower in the New Zealand streams ranging from 0.03 to 5.02 $\mu\text{g cm}^{-2}$ and averaging 1.88 $\mu\text{g cm}^{-2}$ (Table 1). Chlorophyll a declined with decreasing bed stability at the New Zealand sites ($r^2 = 0.17$, $F_{1,22} = 4.46$, $P = 0.046$, $y = 4.04 - 0.06x$), however there was no relationship between stability and chlorophyll a at Spanish sites ($r^2 = 0.06$, $F_{1,22} = 1.36$, $P = 0.26$).

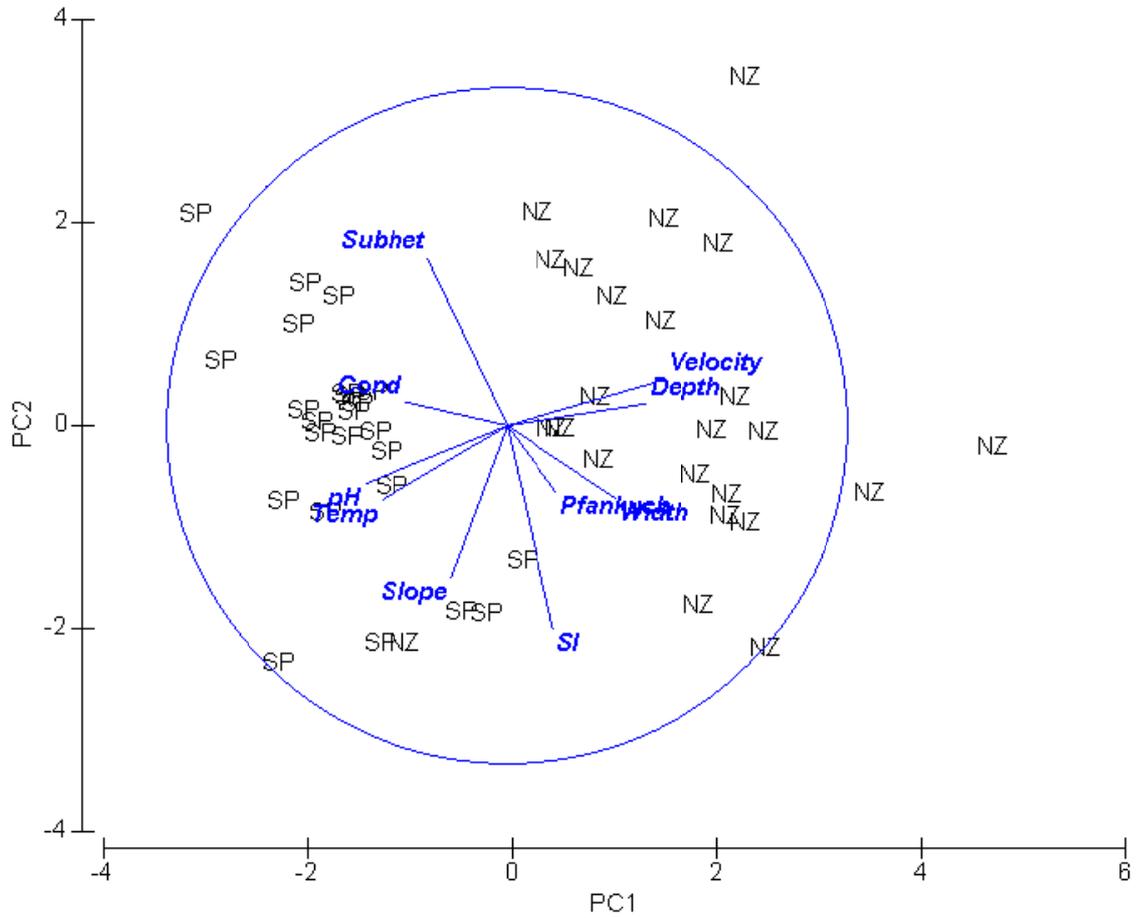


Figure 1: Principal component analysis for environmental variables in 24 streams from each of the central North Island of New Zealand and Cantabrian Mountains, northern Spain, sampled between February and July 2007. PC1 explained 35.6 % and PC2 explained 16.4 % of the variation in the data (Vectors indicate direction of increase in environmental variables). NZ = New Zealand, SP = Spain, SI = substrate size index, Subhet = Shannon substrate heterogeneity, Temp = temperature, Cond = conductivity.

Table 1: Mean (\pm 1 S.E.) physicochemical, periphyton and invertebrate community metrics collected from 24 streams in each of the central North Island of New Zealand and Cantabrian Mountains, northern Spain, between February and July 2007. *F* and *P* values indicate results of one-way ANOVA testing for differences between the two regions. NZ = New Zealand. PC = principle component.

Site	NZ	Spain	<i>F</i> _{1,46}	<i>P</i>
Width (m)	12.9 (1.95)	7.72 (1.24)	5.04	0.03
Depth (cm)	31.05 (1.85)	18.86 (0.98)	33.86	0
Velocity (m s ⁻¹)	0.89 (0.04)	0.4 (0.03)	98.48	<0.0001
Conductivity ($\mu\text{s cm}^{-1}$)	131.58 (14.15)	205.96 (18.91)	9.92	0.003
Temperature (°C)	10.71 (0.45)	15.15 (0.39)	55.98	<0.0001
pH	7.88 (0.12)	8.86 (0.05)	57.09	<0.0001
Substrate size index	152.59 (9.02)	139.11 (6.08)	1.53	0.222
Substrate heterogeneity	1.9 (0.03)	1.98 (0.03)	3.32	0.075
Slope (m 100 m ⁻¹)	3.77 (0.35)	5.18 (0.61)	4.02	0.051
Pfankuch bottom	36.88 (2.12)	32.75 (1.74)	2.27	0.139
PC1	1.6 (1.19)	-1.6 (0.72)	127.57	<0.0001
PC2	0.19 (1.41)	-0.19 (1.13)	1.1	0.3
Chlorophyll <i>a</i> ($\mu\text{g cm}^{-2}$)	1.88 (0.3)	5.84 (0.72)	26.01	<0.0001
No. of taxa	14.78 (1.02)	15.6 (0.59)	0.48	0.491
No. of animals	327.5 (59.52)	928.23 (406.66)	2.14	0.151
Shannon diversity (<i>H'</i>)	1.77 (0.09)	1.63 (0.07)	1.65	0.205
% EPT animals	0.54 (0.06)	0.57 (0.04)	0.24	0.627

Community metrics

We found 76 taxa in Spanish and 82 taxa in New Zealand streams. The mean number of individuals was higher in Spanish than New Zealand streams but due to the high degree of variation this difference was not significant (Table 1). Moreover, the mean number of taxa, Shannon diversity index and the % EPT animals did not differ between New Zealand and Spanish streams (Table 1).

Density, richness and the Shannon index increased log-linearly with increasing levels of chlorophyll *a* in the New Zealand streams (Table 2, Fig. 2). The % EPT animals was not related to chlorophyll *a* in either New Zealand or Spanish streams (Table 2, Fig. 2). The number of animals increased linearly with increasing chlorophyll *a* in the Spanish streams but richness and the Shannon index were not related to chlorophyll *a* in these streams (Table 2, Fig. 2).

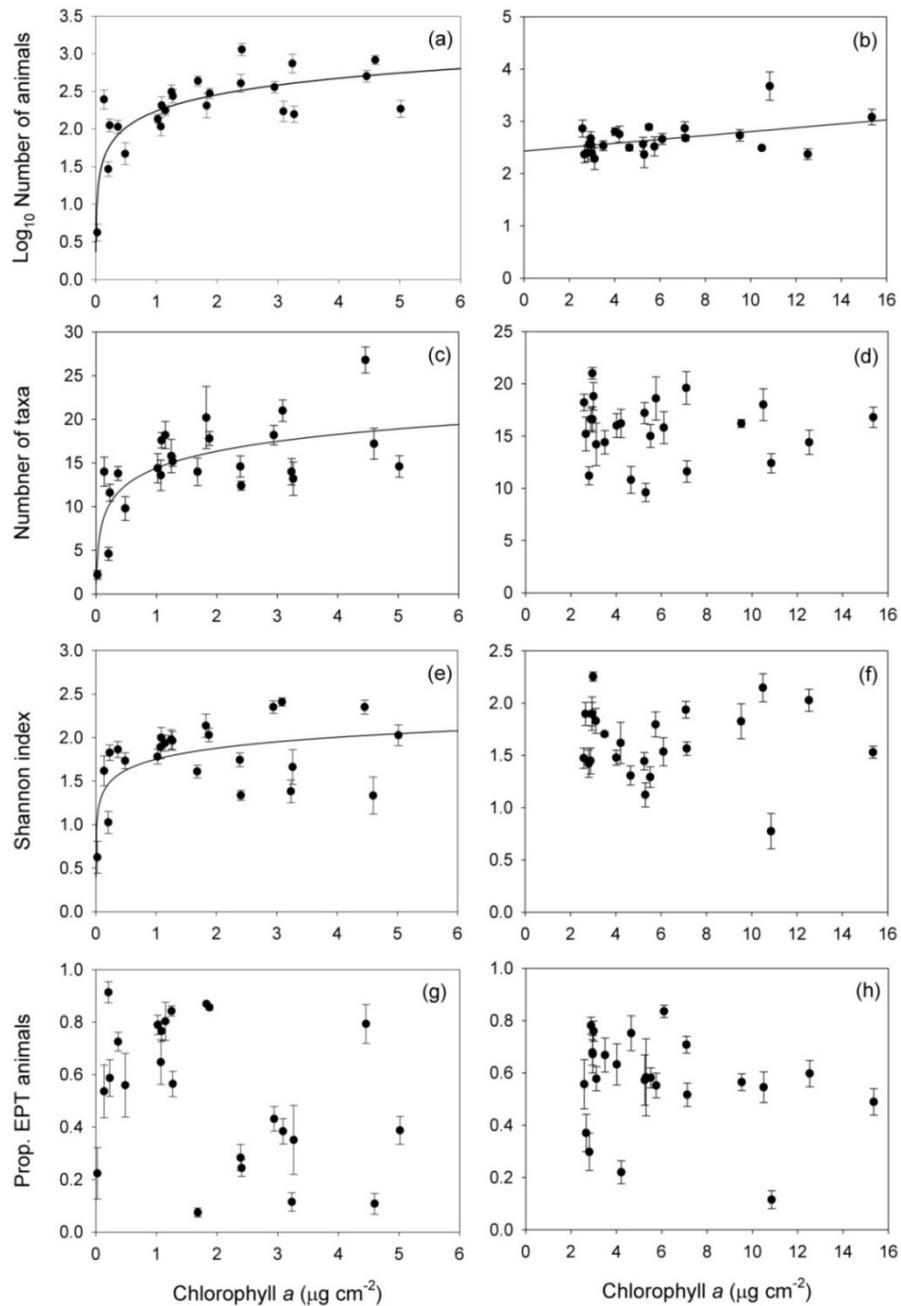


Figure 2: Mean (± 1 S.E.) (a, b) number of animals, (c, d) number of taxa, (e, f) Shannon diversity, and (g, h) proportion of EPT animals as a function of chlorophyll *a* in 24 (a, c, e, g) central North Island, New Zealand and (b, d, f, h) Cantabrian Mountains, northern Spain streams, collected between February and July 2007. Results of regression analysis are presented in Table 2.

Table 2: Results of individual regression analysis of invertebrate community metrics as a function of (a) chlorophyll *a* and (b) the Pfankuch bottom component collected from 24 streams in each of the central North Island of New Zealand and Cantabrian Mountains, northern Spain, between February and July 2007. Degrees of freedom = 1, 22 for linear and log-linear and 2, 21 for quadratic regressions. AIC = Akaike's information criterion where lower numbers represent a better model.

	New Zealand				Spain			
	<i>F</i> (AIC)	<i>P</i>	<i>r</i> ²	Equation	<i>F</i>	<i>P</i>	<i>r</i> ²	Equation
(a) Chlorophyll <i>a</i> (µg cm⁻²)								
Log ₁₀ number of animals	36.07	<0.0001	0.62	$y = 2.24 + 0.31 \cdot \ln(x)$	5.31	0.031	0.19	$y = 2.43 + 0.04x$
Number of taxa	22.93	<0.0001	0.51	$y = 14.41 + 2.79 \cdot \ln(x)$	0.05	0.83	0.002	Non-significant
Shannon index	9.87	0.005	0.31	$y = 1.75 + 0.18 \cdot \ln(x)$	0.04	0.83	0.002	Non-significant
% EPT animals	4.15	0.054	0.16	Non-significant	1.14	0.3	0.05	Non-significant
(b) Pfankuch index								
Log ₁₀ number of animals	12.92 (68.7)	0.002	0.37	$y = 3.38 - 0.03x$	0.68	0.42	0.03	Non-significant
quadratic	9.43 (58.6)	0.001	0.47	$y = 1.64 + 0.07x - 0.001x^2$				
Number of taxa	4.76 (-31.9)	0.04	0.18	$y = 22.24 - 0.2x$	0.19	0.66	0.01	Non-significant
quadratic	13.42 (-32.6)	0.0002	0.56	$y = -10.59 + 1.76x - 0.03x^2$				
Shannon index	1.7 (-32.2)	0.21	0.07	Non-significant	0.78	0.39	0.03	Non-significant
quadratic	7.82 (-39.2)	0.003	0.43	$y = -0.48 + 0.15x - 0.002x^2$				
% EPT animals	1.88	0.18	0.08	Non-significant	0.17	0.69	0.01	Non-significant

Fitting the New Zealand and Spanish invertebrate community metrics together against chlorophyll a showed that the New Zealand streams fit along the lower end of the chlorophyll a gradient and the Spanish streams were at the higher end (Table 3, Fig. 3). Both the number of animals and the number of taxa fit similar log-linear curves to those for the New Zealand data (Table 3, Fig. 3). The Spanish data simply placed further to the right along the curve at higher levels of chlorophyll a (Table 3, Fig. 3).

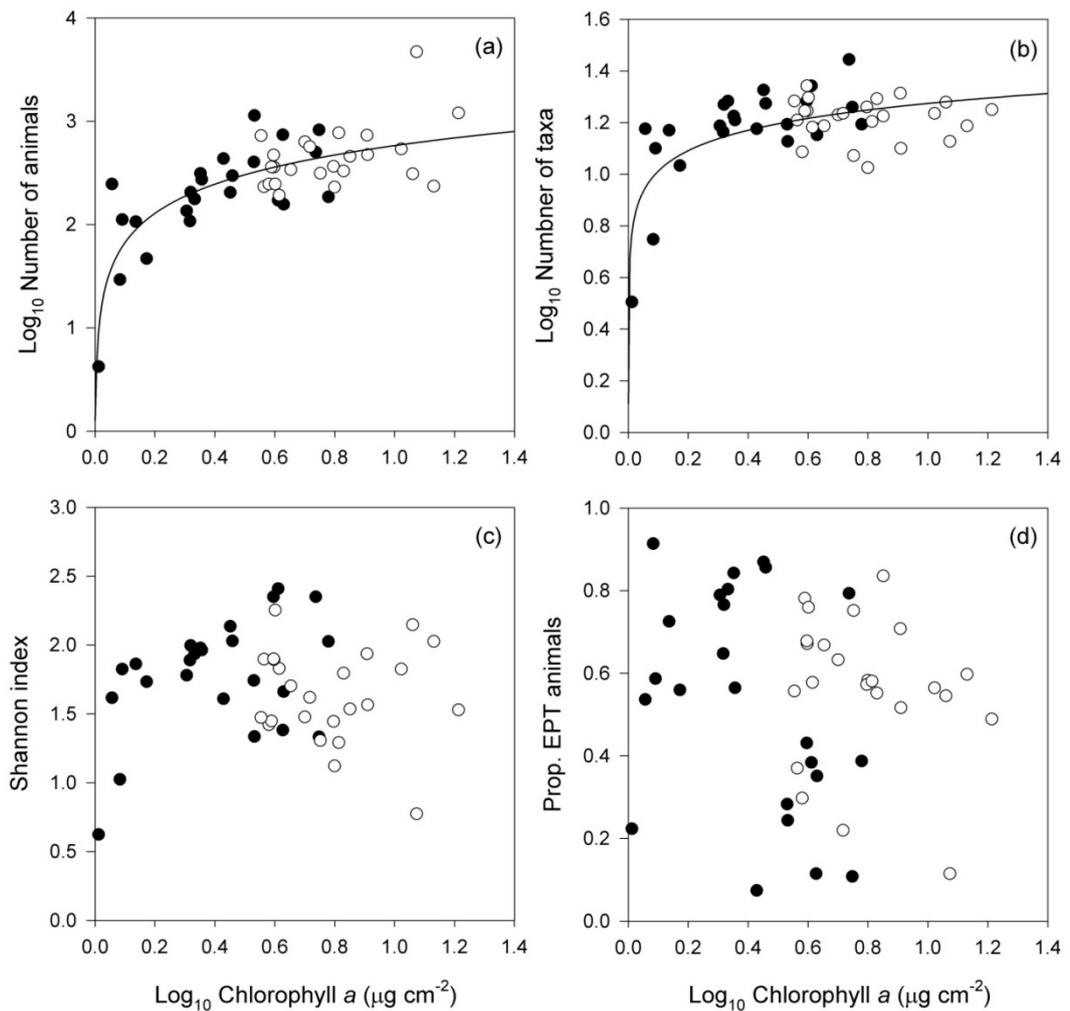


Figure 3: Mean (a) number of animals, (b) number of taxa, (c) Shannon diversity, and (d) proportion of EPT animals as a function of chlorophyll a in 48 central North Island, New Zealand and Cantabrian Mountains, northern Spain streams, collected between February and July 2007. Black symbols are New Zealand streams and white symbols are Spanish streams. Results of regression analysis are presented in Table 3.

Table 3: Results of combined regression analysis of invertebrate community metrics as a function of chlorophyll *a* collected from 48 streams in the central North Island of New Zealand and Cantabrian Mountains, northern Spain, between February and July 2007.

	$F_{1,46}$	P	r^2	Equation
Log ₁₀ number of animals	37.08	<0.0001	0.446	$y = 1.27 + 0.11 \cdot \ln(x)$
Number of taxa	69.88	<0.0001	0.603	$y = 2.77 + 0.41 \cdot \ln(x)$
Shannon index	1.36	0.25	0.029	Non-significant
% EPT animals	0.02	0.89	0.0004	Non-significant

None of the four invertebrate community metrics were related to bed stability in the Spanish sites (Table 2). The number of animals declined at an increasing rate with stability in the New Zealand streams, and taxonomic richness and the Shannon diversity index peaked at intermediate levels of stability in the New Zealand streams (Table 2). A second term yielded a better fit to the data for these metrics in these streams. There was no relationship between stability and % EPT animals in the New Zealand streams (Table 2).

Discussion

While the productivity-diversity relationship is a central theme in many aspects of ecology (Abrams 1995, Waide et al. 1999, Mittelbach et al. 2001), until recently little emphasis has been placed on assessing this relationship in lotic systems. Nonetheless, several recent studies have shown a strong link between the two (Death 2002, Barquin 2004, Death and Zimmermann 2005, Cardinale et al. 2006, Tonkin and Death In prep.-a, Tonkin and Death In Prep.-b, Tonkin et al. In Prep.-a). The prevailing theme in these studies is that the productivity-diversity relationship is log-linear at local scales (but see Death and Zimmermann 2005, Cardinale et al. 2006). That is, productivity appears to set the upper limit to richness in streams (Death 2002). We hypothesized that both regions in this study would follow the same log-linear increase in diversity with productivity. At first glance, New Zealand streams were much more closely linked with productivity and exhibited the same log-linear relationship mentioned above. In contrast, no diversity measure appeared to be related to productivity in the Spanish streams. In fact, the only community metric linked with productivity in the Spanish

streams was the number of animals which increased linearly with productivity. However, differentiation of relationship between the two regions stream communities may simply be a result of sampling at different ranges along the productivity continuum.

Although it appears there are two differing responses of diversity to productivity between the Northern and Southern Hemisphere streams, Spanish streams had roughly three times higher primary productivity than the New Zealand streams. Essentially, the New Zealand streams examined occurred along the first half of the productivity scale and Spanish ones along the second half. Combining the two regions showed density and richness fit the log-linear curve fitted to the New Zealand data, with no evidence of a decline at higher productivity, suggesting this may be a universal pattern. Most prior studies of this nature in New Zealand streams examined the link between productivity and diversity at similar levels of productivity to those here (e.g. Death 2002, Tonkin et al. In prep.-b) suggesting these may be simply covering the lower half of the more common unimodal trend found in other ecosystems. However, Barquin (2004) assessed this relationship in New Zealand streams with up to five times higher productivity than the present study and found no evidence for a decline in richness with increasing productivity. This fits with Death's (2002) postulation that productivity, rather than competitive interactions, sets the upper limit to stream richness. The 'hump shaped' relationship between productivity and diversity is common in many systems, especially with sedentary organisms (Waide et al. 1999, Mittelbach et al. 2001), and has been found in lotic systems when assessing primary producer communities (Cardinale et al. 2006). Rosenzweig (1995) provides several explanations for a decline in richness at greater productivity including competitive exclusion, but stream communities do not often fit within this theory. Nevertheless, competitive exclusion does occur in stream communities (e.g. Hemphill and Cooper 1983), but the influence of these interactions appears to be variable (Reice 1985) and it is more likely in streams with sedentary species (Hemphill and Cooper 1983, McAuliffe 1984). As most stream invertebrate communities are dominated by organisms with a high degree of mobility and immigration and emigration (Downes

1990, Death 2008), unimodal productivity-diversity relationships are rare (but see Death and Zimmermann 2005).

Although the number of taxa increased with increasing productivity, evenness of communities declined. However, this was not a consistent pattern and varied greatly at higher levels of productivity. Within low productivity streams, Death (2002) found diversity measures which account for community evenness are also positively linked with productivity. However, two recent studies which found log-linear increases in richness with productivity (Tonkin and Death In prep.-a, Tonkin et al. In prep.-b), show that accounting for both evenness and density removed any relationship. In fact, combining the New Zealand and Spanish data indicated the response of dominance to productivity was highly variable. Tonkin et al. (In Prep.-a) show that these Spanish communities become increasingly dominated by *Prosimulium* spp. at greater productivity as a result of the high proportion of filamentous algae in these streams. That is, although black flies (Simuliidae) do not graze directly upon algae they can be found in high densities feeding on drifting algal cells (Peterson et al. 1985), as well high densities of smaller individuals attached to filamentous algae (Dudley et al. 1986). Tonkin et al. (In Prep.-a) propose that within streams, the productivity-diversity relationship is heavily influenced by the taxonomic composition of the algal communities. However, although communities became more dominated, competitive exclusion does not appear to occur. Several other lotic studies have also found early colonisers remain after later colonisers arrive and are not displaced (Death 1996, Collier and Quinn 2003, Death 2006).

The % EPT index is commonly used as a bioassessment tool in streams (e.g. Lenat 1988, Barbour et al. 1999) as these taxa are considered pollution sensitive. However, both within each region and combined, the response was highly variable. Tonkin et al. (In Prep.-a) found the percent of EPT animals responds more strongly to algal community composition than productivity. If eutrophication only leads to an increase in productivity, the EPT metric is unlikely to indicate this in our study streams but if it affects the type of algae it will. In the New Zealand streams, although richness increased along a log-linear gradient, there appeared to be a strong shift in the community from EPT dominated to chironomid dominated at roughly the midpoint on

the productivity gradient. However, when compared to the Spanish streams, this shift in community composition occurred at relatively low levels of productivity which is likely to be due to the alpine nature of this environment. Specifically, certain chironomids are able to tolerate these types of environments such as cold water and instability and thus appear at lower levels of productivity (Milner and Petts 1994).

Productivity is linked strongly with disturbance in streams (Lake 2000, Death 2002, Cardinale et al. 2006, Tonkin and Death In prep.-a, Tonkin et al. In prep.-b). Consequently, we expected that bed stability could provide explanations for variation in the productivity-diversity relationship. However, traditional models that require a trade-off of competitive and colonizing ability in taxa such as the DEM (Huston 1979, 1994, Kondoh 2001), do not find much support in streams (Tonkin and Death In prep.-a, Tonkin et al. In prep.-b), but see Cardinale et al. (2006). Our results indicate that New Zealand stream communities respond strongly to bed stability but Spanish streams do not. In fact, the Pfankuch index was not able to predict any of the invertebrate community metrics in Spanish streams and thus stability was not able to explain the lack of productivity-diversity relationship in Spanish streams. Barquin and Death (2006) found diversity of benthic invertebrates were higher in more stable habitats in New Zealand streams but Barquin and Death (2004) found the opposite in Spanish streams. New Zealand stream communities are highly dependent on both productivity and disturbance for the maintenance of diversity (Death 2002, Tonkin et al. In prep.-b), but these studies suggest the role of disturbance is simply to reset the colonization process (at different rates) allowing habitats to be recolonised. Richness is consequently governed by productivity through the processes discussed previously; however this was not exhibited in the Spanish streams which may be due to a lack of low productivity sites in the limited range of study sites.

The lack of focused assessments of the productivity-diversity relationship in lotic systems has left benthic ecologists with no clear idea of the nature of the relationship. With the strong role productivity plays in streams, especially in conjunction with disturbance (Lake 2000, Death 2002, Cardinale et al. 2006, Tonkin and Death In prep.-a, Tonkin et al. In prep.-b), it is essential to elucidate this relationship. As has been found in recent studies (Death 2002, Barquin 2004, Tonkin

and Death In prep.-a, Tonkin et al. In prep.-b), we suggest the role of productivity is indeed to dictate maximum richness in streams rather than to increase the effect of competitive interactions. Although variation in response between the two regions was evident in this study, the overall relationship when combining regions suggests that Death's (2002) postulation of productivity setting the upper limit to richness in streams is correct. The variable response found between the two regions indicates that caution is required when interpreting results along differing scales of environmental variation. With the large range of productivity assessed in this study and no decline in richness at high levels of productivity, we provide strong evidence that the DEM is unlikely to be relevant in streams.

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Appendix 1: Latitude, longitude and altitude of 48 streams sampled in the central North Island of New Zealand and Cantabrian Mountains of northern Spain, between February and July 2007.

New Zealand				Spain			
Site	Longitude	Latitude	Alt.	Site	Longitude	Latitude	Alt.
Mangatoetoenui @ SH1	175.7316156	-39.2363068	971	Rio Besaya @ Helguera	-4.03276	43.158628	214
Whakapapa d/s intake	175.4659706	-39.11992199	680	Rio Eracia @ Helguera	-4.030378	43.159622	222
Whakapapaiti @ SH4	175.4720796	-39.17692963	859	Rio Bisuena @ Barcena Pie de Concha	-4.06826	43.121292	309
Trib of Ohinepango @ old hut	175.671968	-39.20895258	1106	Torina @ Barcena Pie de Concha	-4.054722	43.126793	299
Waihohonu Springs	175.6654827	-39.18896035	1158	Santiurde @ Santiurde	-4.078611	43.063231	634
Wahianoa stream u/s intake	175.6407765	-39.38396292	934	Rumadero @ Pesquera	-4.074784	43.083177	574
Te Unuunuakapuataeariki stream	175.5593075	-39.4431139	701	Rio Leon @ San Martin de Quevedo	-4.038779	43.139996	264
Tongariro d/s Poutu intake	175.8224059	-39.13002278	456	Ayo Valdeiguna @ Pedredo	-4.067773	43.192911	185
Waipakahi @ end of road	175.7729642	-39.22440144	857	Rio Argoza @ Barcena Mayor	-4.232753	43.156963	422
Mangatepopo by camp	175.5633283	-39.06976046	752	Rio Saja @ Renedo	-4.30455	43.194076	293
Mangatepopo d/s dam	175.5523842	-39.05335106	624	Rio de la Magdalena @ San Andres	-3.897027	43.096378	412
Ohinepango Springs	175.6779304	-39.21838435	1091	Ayo Salcera @ San Miguel de Luena	-3.899921	43.112736	347
Mangaturuturu river	175.3917215	-39.30696099	820	Rio Viaña @ Viaña	-3.804674	43.155633	326
Tongariro d/s Rangipo dam	175.779722	-39.21008569	813	Rio Pas @ Pandillo	-3.759107	43.164859	366
Tongariro @ pillars of hercules	175.7881839	-39.18527209	660	Llerana @ Coterillo	-3.794589	43.263832	207
Whanganui @ Te Porere	175.5924007	-39.04622437	654	Rio Pisuena @ Barcena de Carriedo	-3.823485	43.241998	181
Whanganui ds intake	175.6010392	-39.01997827	604	Nansa @ Puenteansa	-4.406832	43.257111	168
Oturere Stream SH1	175.7576087	-39.18382654	809	Ayo de Hoyamala @ Puenteansa	-4.406179	43.257101	163
Unnamed @ SH1	175.7578776	-39.1940232	885	Lamasón @ Quintanilla	-4.476253	43.25448	238
Whakapapanui @SH4	175.5090823	-39.1491875	835	Ayo de Traveseras @ Quitanilla	-4.30588	43.256427	239
Unnamed Karioi forest stream	175.6278138	-39.38270332	935	Palomba @ Paracuelles	-4.211634	43.019856	895
Poutu Stream	175.7969903	-39.07827181	518	Rio Hajar @ Espanilla	-4.226527	43.019571	937
Tauwhitikuri Stream d/s intake	175.5513666	-39.05365336	621	Rio Rucebos @ Soto	-4.222249	43.035916	960
Makomiko stream	175.3923096	-39.23638244	746	Rio Guares @ Abiado	-4.289066	43.016011	1061

Chapter 6

Scale dependent effects of productivity and disturbance on diversity



Abstract

The effects of productivity and disturbance on diversity are highly variable with the spatial scale at which they are examined. Not only do productivity and disturbance have strong influences on diversity patterns at local and regional scales but they can affect the way in which communities assemble and in turn alter beta diversity or community dissimilarity. We assessed whether the form of both the productivity- and disturbance-diversity relationships differed between the spatial scale at which they were examined using experimental stream channels in three Hawke's Bay, New Zealand, streams. In place of true local and regional richness, we used the proxies within- and between-stream richness, as well as assessing between-stream community dissimilarity (similar to beta diversity). Our results indicate that productivity and disturbance both affect diversity but at individual scales and in different forms. At the within-stream scale, richness was a u-shaped function of productivity whereas at the between-stream scale richness increased monotonically with increasing productivity. Community dissimilarity on the other hand, increased monotonically with increasing rate of disturbance. Rather than a greater role of deterministic assembly with increasing disturbance, our results indicate the opposite but it appears that communities are simply converging on those found in the surrounding streambed with time since disturbance. Specifically, communities were more similar within individual streams than within disturbance treatments and those to colonise post-disturbance were simply a subset of taxa present at each site regardless of perceived colonising ability rather than a suite of specialist colonising taxa. These results demonstrate that without a distinction between early and late colonisers, a greater rate of deterministic assembly at high disturbance will not occur.

Introduction

The relationship between productivity and diversity can be highly variable (Currie 1991, Abrams 1995, Waide et al. 1999, Mittelbach et al. 2001). Unimodal (e.g. Grime 1973a, Huston 1979, Rosenzweig 1992, 1995, Leibold 1999, Waide et al. 1999, Mittelbach et al. 2001) or linear (e.g. Currie and Paquin 1987, Currie 1991, Abrams 1995, Waide et al. 1999, Gaston 2000, Mittelbach et al. 2001) increases in diversity with increasing productivity are those most often observed. However, linear declines, u-shaped relationships and no relationship also occur (Waide et al. 1999, Mittelbach et al. 2001). One explanation for the different outcomes is the difference in the spatial scale of sampling (Currie 1991, Chase and Leibold 2002). Smaller scale studies commonly find unimodal relationships between productivity and diversity but at increasing spatial scales the pattern is often one of monotonic increases in diversity with productivity (Waide et al. 1999, Mittelbach et al. 2001). There are many mechanisms postulated to lead to this unimodal relationship (Rosenzweig and Abramsky 1993, Abrams 1995, Waide et al. 1999). For example, Kassen et al. (2000) have shown niche specialisation in heterogeneous, but not homogeneous environments can cause this pattern. Chase and Leibold (2002) also found differences in the nature of the relationship when considered from different scales; a hump shaped trend occurred at local scales, a linear pattern at the regional scale and community dissimilarity increased with productivity.

The mechanisms underlying the differences in the relationship between productivity and diversity remain uncertain, although many have been hypothesised and these are also likely to vary with scale (Waide et al. 1999). Two factors thought to strongly influence the productivity-diversity relationship are disturbance (Huston 1979, 1994, Kondoh 2001), and the history of community assembly (Fukami and Morin 2003). The disturbance-diversity relationship also varies with spatial and temporal scale (Petraitis et al. 1989, Mackey and Currie 2001, Chase 2007). However the prevailing theme in disturbance ecology revolves around the Intermediate Disturbance Hypothesis (IDH) (Grime 1973b, Connell 1978, Sousa 1979), and recently Roxburgh et al. (2004) have shown the promotion of richness at intermediate levels of disturbance

can come from many mechanisms. But the requirement for a competition-colonisation trade-off (Chesson and Huntly 1997, Roxburgh et al. 2004, Cadotte 2007), and the fact that this has been found to be lacking in many ecosystems, has led many to suggest disturbance simply removes taxa (Death and Winterbourn 1995). Many have advocated that diversity is a function of the interaction between disturbance and productivity (Huston 1979, 1994, Kondoh 2001, Cardinale et al. 2006), however recent empirical work suggests the effects are additive (Tonkin and Death In prep., Tonkin et al. In prep.).

Both productivity and disturbance can also alter β diversity and community dissimilarity through changes in assembly sequences (Chase 2007, Lepori and Malmqvist 2009, Chase 2010). Deterministic assembly involves the recruitment of colonists from the regional pool based on niche preferences, whereas stochastic assembly involves random selection of available colonists (i.e. ecological drift). The debate on whether deterministic (Poff 1997) or stochastic determinates (Reice 1994, Hubbell 2001) are more important is long standing, though it is likely that a combination of both occur (Hart 1992, Thompson and Townsend 2006). Recently, Chase (2010) suggested that more productive environments lead to higher β diversity through a stronger dependence on stochastic, as opposed to deterministic, community assembly. Deterministic assembly processes will likely be more prevalent in harsh environments where conditions filter out unsuitable taxa; benign environments on the other hand will be governed by more stochastic processes allowing for a greater representation of the regional pool (Chase 2007). This suggests β diversity or community dissimilarity will decline with disturbance rate as a limited range of more specialist traits are required in more disturbed habitats. Nonetheless, Lepori and Malmqvist (2009) found deterministic control (and associated lowest β diversity) was greatest at intermediate levels of disturbance suggesting a more complex interplay between stochastic and deterministic control.

We set out to test the effect of spatial scale on both the productivity-diversity and disturbance-diversity relationships using experimental stream channels. Rather than true α , β and γ diversity, we used within- (local) and between-stream (regional) richness and between stream community dissimilarity (β diversity) for each

disturbance and productivity treatment. Based on previous work suggesting productivity sets the upper limit to diversity in streams (Death 2002, Tonkin and Death In prep., Tonkin et al. In prep.), we predict that within-stream taxonomic richness will increase log-linearly with productivity and between-stream richness will increase monotonically (Chase and Leibold 2002). As there is no clear competitive-colonisation trade-off in New Zealand stream invertebrate communities (Death and Winterbourn 1995, Death 2002), we hypothesise that within-stream richness will decline with disturbance. Although there is support for increased diversity with disturbance at the regional scale, as it allows for the representation of early colonising species within patchy environments (Hastings 1980, Pickett and White 1985, Chesson and Huntly 1997), we predict between-stream richness should match within-stream richness and decline. This is because between-stream richness was assessed at the same disturbance rate, thus disturbance should theoretically be homogeneous. We expect greater dissimilarity in community composition (β diversity) at lower rates of disturbance as a result of more stochastic assembly processes (Chase 2003, 2007). The scale of this study is such that connectivity between replicates is low which has been found to confound diversity assessments (Warren 1996, Chase 2003, Chase and Ryberg 2004, Ostman et al. 2006, Matthiessen et al. 2010).

Methods

Study sites and physicochemical measures

Pastoral farming and wine production dominates land-use of Hawke's Bay, in the East of the North Island of New Zealand; an area characterised by a warm and dry climate with a mean annual rainfall of 783 mm. Three spring-fed streams of relatively similar characteristics (mean width: 1.5-4.7 m; mean depth: 0.15-0.44 m; mean velocity: 0.42-1.52 m s⁻¹) were selected for use in this study in the Ruataniwha Plains. Temperature and conductivity in these streams ranged from 15.2 to 17.9°C and 160 to 220 $\mu\text{S cm}^{-1}$ respectively during the experimental period and streams range in altitude from 134 to 146 m a.s.l..

Experimental methods

Eight plastic channels (1500 mm long x 150 mm wide x 100 mm deep) were placed in the bed of each stream and filled with cobbles. Cobbles were sourced from within the stream bed and allowed to acclimatise for 21 days before the treatment period. Four disturbance and two productivity treatments were applied within each stream. The disturbance treatments were: no disturbance (after initial disturbance at day 0), every 16, 8, and 4 days; and productivity treatments were either high or low. This yielded eight treatments: the four levels of disturbance each at low and high productivity levels. Productivity was characterised as high or low based on the presence or absence of shading. Shade was applied by covering four of the channels in each stream with 1800 mm x 350 mm metal sheeting approximately 200 mm above the substrate and held in place with metal stakes and rubber grommets. Disturbance was performed by physically stirring the full contents of the channel whilst minimising removal of periphyton on the substrate for two minutes. However, larger forms of macroalgae were inevitably removed, if present, due to their ease of detachment.

Sampling protocols

Invertebrates were sampled from three random 250 mm sections within each channel. Sampling was performed with a modified section of guttering, similar to the artificial channels, with a 250 μ m mesh net attached. One stone (α axis < 60 mm) was removed from each replicate for later analysis of periphyton biomass. The remaining sample was placed in 70 % ETOH and later identified in the laboratory using available keys (e.g. Towns and Peters 1996, Winterbourn et al. 2000).

Primary productivity was estimated from measures of chlorophyll *a* on stones from within each sample. Chlorophyll *a* of natural substrate and primary productivity in streams are highly correlated (Morin et al. 1999, Tonkin and Death In prep.). Stones were kept cool and dark on ice in the field before being stored at -20°C. Photosynthetic pigments were extracted from stones 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* pigment concentration

using Steinman and Lamberti (1996). These were then corrected for stone surface area (Graham et al. 1988) and halved to account for periphyton being present only on upper stone surfaces.

Statistical analysis

Within-stream ('local') taxonomic richness was calculated as the pooled number of taxa for the three samples within each treatment. Between-stream ('regional') richness was calculated as the total number of taxa for the three samples within each treatment and each stream (nine samples). This is not true regional richness (γ) but a surrogate as it is simply the total number of taxa in all three streams for each treatment, thus we use the terms within- and between-stream richness. We calculated the dissimilarity in community composition in treatments between streams. These dissimilarity metrics left us with three pairwise comparisons which were averaged to achieve a 'regional' dissimilarity metric. Dissimilarity (100 – similarity) was estimated using the Bray-Curtis similarity metric in Primer v6 (Clarke and Gorley 2006). This method takes into account variation in taxonomic abundance and was performed on raw data. Although this metric is similar conceptually to β diversity, it is a measure of community dissimilarity accounting for abundances rather than the number of unique taxa to each community. Thus, if dissimilarity is zero, all taxa are shared and at the same abundances between all communities and if dissimilarity is 100 then no taxa are shared. In order to assess whether changes in taxonomic richness with productivity and disturbance were due to changes in the density of animals, we also calculated the number of individuals and rarefied taxonomic richness.

To assess one factor of resource heterogeneity we calculated variation in productivity between replicates and streams by summing the differences between chlorophyll *a* values with each treatment. Similarity Percentages (SIMPER) was used to assess which taxa contributed the greatest to differences between and within treatments using Primer v6. Linear and quadratic regression was performed in order to test for relationships between productivity, disturbance and diversity at the three spatial scales using Statistix (Statistix 8 ©, Analytical Software, Tallahassee, FL, U.S.A.). The effects of productivity and stability based on *a priori* group selection were

assessed using two-way crossed Analysis of Variance (ANOVA) design in Statistix. Both productivity and stability were treated as fixed factors.

Results

Chlorophyll *a* was higher in all high productivity treatments ($F_{1,22} = 4.36, P = 0.049$), but did not differ with disturbance rate ($F_{3,20} = 0.75, P = 0.54$). The number of taxa did not differ with disturbance rate ($F_{3,16} = 0.33, P = 0.81$), productivity ($F_{1,16} = 0.15, P = 0.7$), or an interaction between the two ($F_{3,16} = 0.13, P = 0.93$).

Within-stream taxonomic richness exhibited a u-shaped quadratic response to increasing productivity (Fig. 1, Table 1). This u-shaped relationship between productivity and richness at the local scale can be explained by two separate relationships related to the productivity treatment. In the low productivity treatments, richness declined at a decreasing rate with increasing productivity ($r^2 = 0.68, F_{2,9} = 9.53, P = 0.01, y = 15.2 - 20.82x + 18.62x^2$). In the high productivity treatments, richness increased monotonically although only at the 1 % level ($r^2 = 0.32, F_{1,10} = 4.74, P = 0.06, y = 8.84 + 3.58x$). Richness declined monotonically with productivity at medium disturbance sites (8 day disturbance rate) ($r^2 = 0.94, F_{1,4} = 59.81, P = 0.002, y = 13.38 - 6.2x$) but was not related at any other disturbance rate.

Table 1: Results of linear and quadratic regression analysis for (a) productivity- and (b) disturbance-diversity relationships at within- and between-stream scales and community dissimilarity (100 – Bray-Curtis dissimilarity) in artificial channels in Hawke’s Bay, New Zealand streams, December 2009.

	<i>F</i>	<i>P</i>	<i>r</i> ²	Equation
(a) Productivity				
Within-stream richness	4.98	0.02	0.32	$y = 13.25 - 23.27x + 11.49x^2$
Between-stream richness	16.68	0.007	0.74	$y = 14.42 + 8.76x$
Community dissimilarity	0.025	0.88	0.004	$y = 66.13 + 4.46x$
(b) Disturbance				
Within-stream richness	0.01	0.92	0.0004	$y = 10.75 + 0.03x$
Between-stream richness	0.028	0.87	0.005	$y = 18.5 + 0.1x$
Community dissimilarity	10.16	0.02	0.63	$y = 48.71 + 7.85x$

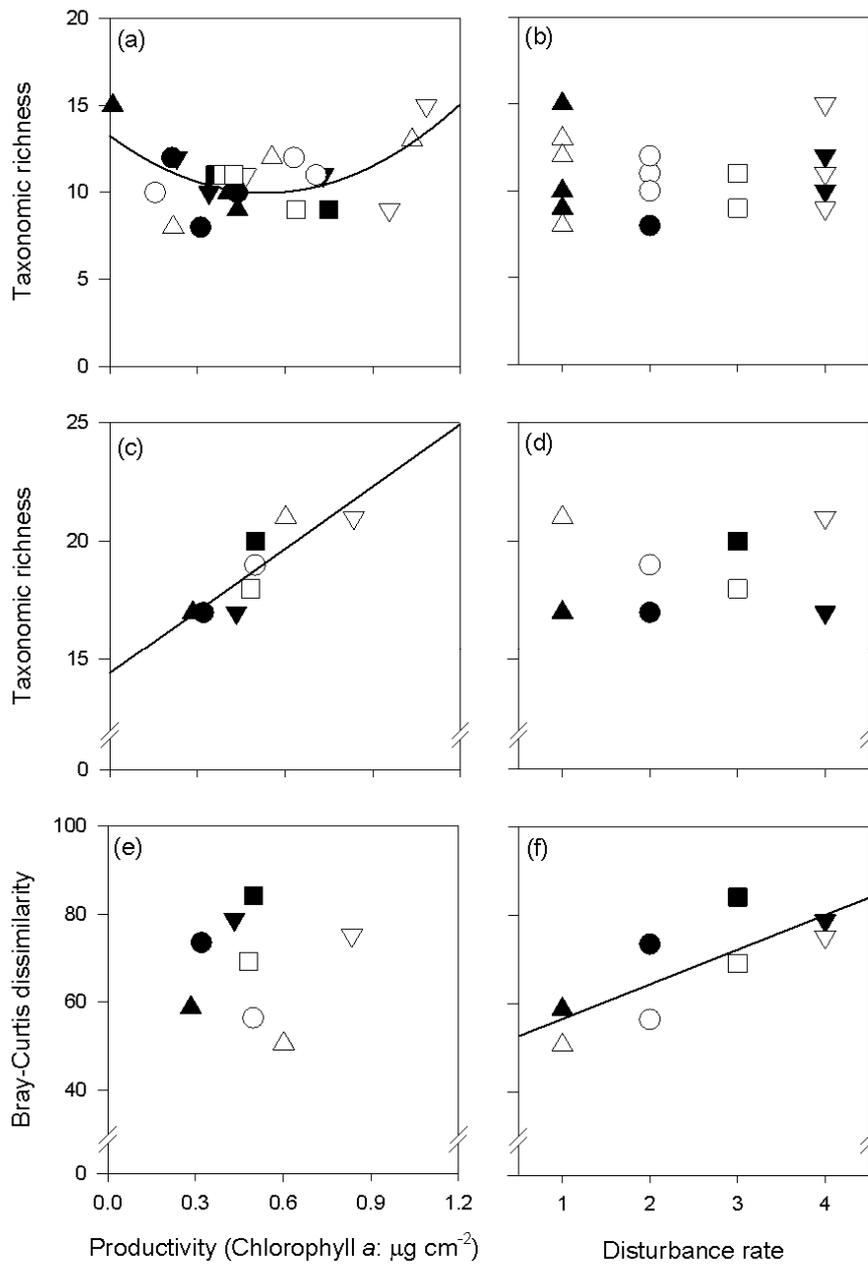


Figure 1: Linear and quadratic regression between diversity and (a, c, e) productivity and (b, d, f) disturbance at (a, b) within- and (c, d) between-stream scales and (e, f) community dissimilarity (100 – Bray-Curtis dissimilarity) in artificial channels in Hawke’s Bay, New Zealand streams, December 2009. Community dissimilarity points represent the average of two-way comparisons for each treatment between streams. Open symbols represent high productivity and closed low productivity treatments. Upright triangles represent disturbance rate of 1 (not disturbed), circles 2 (every 16 days), squares 3 (every 8 days), and inverted triangles 4 (every 4 days).

Between-stream richness increased monotonically with increasing productivity (Fig. 1, Table 1). However, community dissimilarity was not related to productivity. The average variation in productivity (a surrogate for resource heterogeneity) increased with increasing productivity but was not significant ($F_{1,6} = 3.33$, $P = 0.12$). Rarefied richness was not related to productivity at this scale ($F_{1,6} = 0.05$, $P = 0.83$), but the number of animals also increased with productivity at the 1 % level ($r^2 = 0.44$, $F_{1,6} = 4.71$, $P = 0.07$, $y = 28.8 + 108.38x$).

Within- and between-stream richness were not related to disturbance rate but community dissimilarity increased monotonically with increasing rate of disturbance (Fig. 1, Table 1). The number of individuals increased with disturbance rate at the between-stream level ($r^2 = 0.52$, $F_{1,6} = 6.52$, $P = 0.04$, $y = 40.03 + 16.94x$). However, although community dissimilarity showed a slight increase with increasing number of animals per treatment, this was not significant ($F_{1,6} = 3.56$, $P = 0.11$). Likewise, rarefied richness was not related to disturbance ($F_{1,6} = 0.06$, $P = 0.82$). Resource heterogeneity (productivity variation) within treatments did not increase with disturbance ($F_{1,6} = 0.15$, $P = 0.71$). Taxonomic richness increased with increasing variation in productivity but was only significant at the 1 % level ($r^2 = 0.47$, $F_{1,6} = 5.35$, $P = 0.06$, $y = 15.84 + 3.08x$). Taxonomic dissimilarity was not related to variation in productivity ($F_{1,6} = 2.04$, $P = 0.2$).

Overall community structure differed between the four disturbance treatments ($R = 0.06$, $P = 0.03$; Fig 2a). However differences between disturbance treatments were largely due to shifts in density of the most abundant taxa rather than change in composition (SIMPER; Fig. 2; Fig. 3). Five taxa contributed on average 77 % to differences between disturbance treatments. These were: the snail *Potamopyrgus antipodarum*, Oligochaeta, Platyhelminthes, the mayfly *Deleatidium* spp. and the net spinning caddisfly *Aoteapsyche colonica*. The caddisfly *Pycnocentroides aeris* was one of the most abundant taxa at all sites and treatments (7.3 – 27.6 % contribution) but contributed little to differences between sites and disturbance treatments. Of the top five taxa differentiating treatments, *P. antipodarum* (Fig. 2c) and *A. colonica* (Fig. 2d) were the only taxa to respond linearly to disturbance at the between-stream scale and were negatively correlated with each other at both the within-stream scale ($r = -0.45$, P

= 0.03) and between-stream scale although only at the 1 % level ($r = -0.67$, $P = 0.07$; Fig. 3). However, when assessing abundances at each individual site, the responses to disturbance treatment were site specific and varied greatly.

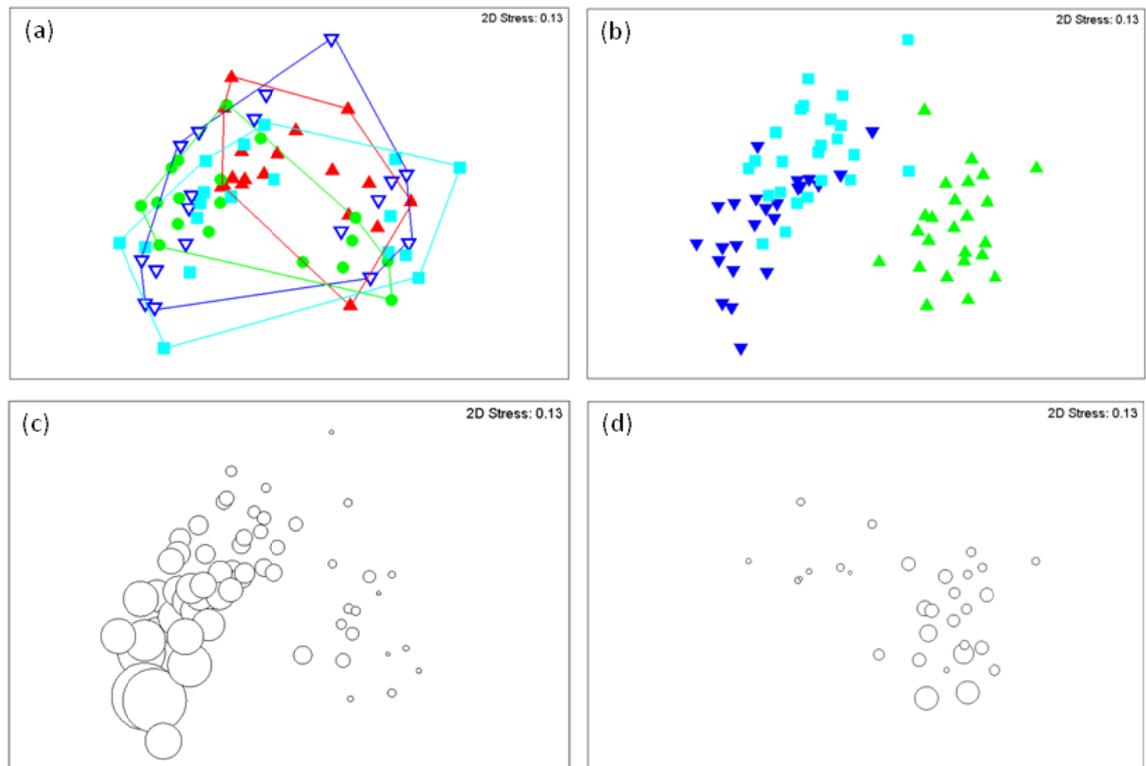


Figure 2: Non-metric multidimensional scaling (NMDS) ordination of axis one against axis two on raw invertebrate community data from artificial stream channels in Hawke's Bay, New Zealand streams, December 2009 (stress = 0.13). (a) Coded based on disturbance treatment: upright triangles = disturbance rate 1 (not disturbed), circles = disturbance rate 2 (every 16 days), squares = disturbance rate 3 (every 8 days), and inverted triangles = disturbance rate 4 (every 4 days). (b) Coded on individual streams: upright triangles = EX1, inverted triangles = EX2, and squares = EX3. (c) Bubble plot for abundance of *Potamopyrgus antipodarum* and (d) *Aoteapsyche colonica*. Bubble scale for both = 0 – 300 individuals per sample.

Community structure of undisturbed treatments (dist. 1) were significantly different to all other treatments (dist. 2: $R = 0.11$, $P = 0.03$; dist. 3: $R = 0.08$, $P = 0.047$; dist. 4: $R = 0.12$, $P = 0.01$; Fig. 2b). However, there was no difference in community structure between the remaining treatments (dist. 2/dist. 3: $R = 0.02$, $P = 0.22$; dist. 2/dist. 4: $R = 0.05$, $P = 0.09$; dist. 3/dist. 4: $R = -0.01$, $P = 0.52$). Variation within disturbance treatments indicated the number of taxa contributing to differences

between replicates declined with disturbance rate. Four taxa (*P. antipodarum*, *A. colonica*, *Pycnocentroides aeris* and *Deleatidium* spp.) each contributed greater than 10 % to differences at the lowest disturbance rates whereas *P. antipodarum* was the only taxa to contribute greater than 10 % at high disturbance sites. The contribution of *P. antipodarum* to differences between replicates increased with disturbance rate.

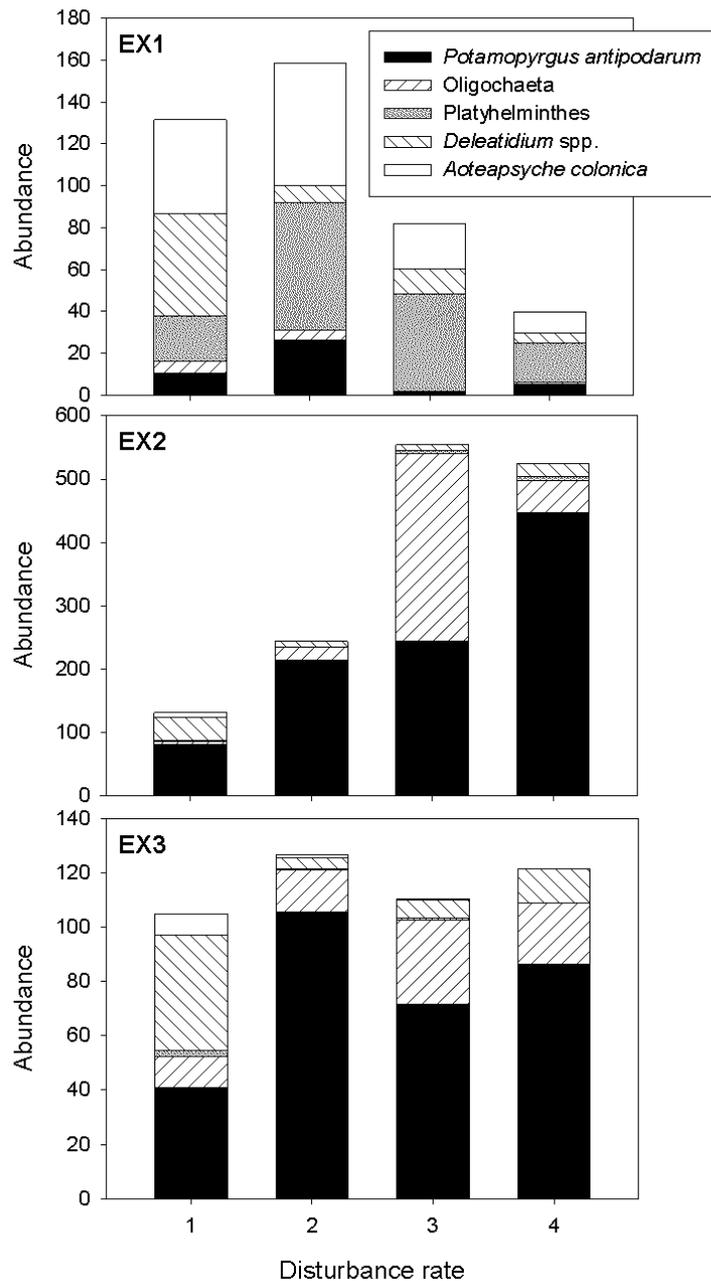


Figure 3: Mean abundance of five taxa contributing the greatest to difference between disturbance treatments at each disturbance treatment collected within artificial channels in three streams (EX1 – EX3) in Hawke’s Bay, New Zealand, December 2009.

P. antipodarum was the most abundant taxa throughout all treatments but abundance of this snail was lowest at the least disturbed treatments (N = 44) and highest at the most disturbed (N = 180) and average per treatment increased with disturbance rate ($r^2 = 0.55$, $F_{1,6} = 7.34$, $P = 0.04$, $y = 11.75 + 39.77x$; Fig. 2c; Fig. 3). However, differences in *P. antipodarum* were not significant between disturbance treatments ($F_{3,20} = 0.98$, $P = 0.42$). *A. colonica* declined monotonically with increasing disturbance ($r^2 = 0.79$, $F_{1,6} = 22.37$, $P = 0.003$, $y = 28.42 - 6.3x$). *P. antipodarum* was negatively correlated with both axis 1 ($r = -0.67$) and axis 2 ($r = -0.45$) of the NMDS ordination (Fig. 2c). *A. colonica* was positively correlated with axis 1 ($r = 0.58$) and negatively correlated with axis 2 ($r = -0.36$; Fig. 2d). *P. antipodarum* was highest at site EX2 (mean = 247 ind./sample) and lowest at site EX1 (mean = 11 ind./sample) ($F_{2,21} = 12.6$, $P = 0.0003$). *A. colonica* was highest at EX1 (mean = 34 ind./sample) and lowest at both EX2 and EX3 (mean = 2 ind./sample) ($F_{2,21} = 15.57$, $P = 0.0001$).

The difference in community structure was more strongly related to individual site differences in composition ($R = 0.65$, $P = 0.001$; Fig. 2b). Communities were more similar at each site regardless of disturbance rate (Bray-Curtis similarity = 46.6 – 50.1) than between disturbance treatments at all sites (Bray-Curtis similarity = 28.6 – 40.7). Moreover, when assessing differences in community composition using presence/absence data, communities were more similar at each site regardless of disturbance rate (Bray-Curtis similarity = 61.5 – 68.3) than between disturbance treatments at all sites (Bray-Curtis similarity = 54.7 - 57).

Discussion

The response of diversity to both productivity and disturbance varied with the spatial scale at which it was examined in this experiment. This is a common phenomenon when assessing these relationships (Petraitis et al. 1989, Currie 1991, Mackey and Currie 2001, Chase and Leibold 2002). In fact, diversity only responded to one of productivity or disturbance at each scale. Productivity affected taxonomic richness at within- (local) and between-stream (regional) scales and disturbance affected community dissimilarity (β diversity). Previous studies have shown that productivity

and disturbance can both affect diversity (e.g. Tonkin and Death In prep., Tonkin et al. In prep.). Although central models in community ecology such as the IDH and DEM predict the disturbance-diversity relationship is humped (Grime 1973b, Connell 1978, Huston 1979, 1994, Kondoh 2001), there is a large body of evidence to suggest diversity simply declines with increasing disturbance (Death and Winterbourn 1995, Vinson and Hawkins 1998, Mackey and Currie 2001, Death 2002), but this relationship can vary with spatial and temporal scale (Petraitis et al. 1989). We predicted diversity in these streams at all scales would decline with increasing rate of disturbance but there was no effect of disturbance at within- and between-stream scales. Although experimental studies have struggled to isolate the effects of disturbance and productivity (Robinson and Minshall 1986, Death 1996), we were able to manipulate productivity independent of disturbance as chlorophyll *a* remained higher in high productivity treatments. The fact that productivity and disturbance are particularly linked in lotic systems suggests conclusions drawn from this paper are not limited to these systems (Lake 2000, Death 2002).

Productivity-diversity relationship

The likelihood of occurrence of u-shaped relationships between productivity and diversity, as found here at the within-stream scale, increases with spatial scale (Mittelbach et al. 2001). Identifying causes for this pattern is difficult as it is not supported by theory and the mechanisms have not been discussed (Mittelbach et al. 2001). Most emphasis is placed on identifying humped trends as much of ecological theory predicts this (Mittelbach et al. 2001), but there are reasons to expect other forms of this relationship (Abrams 1995). The more common unimodal relationship at local scales (e.g. Grime 1973a, Huston 1979, Rosenzweig 1992, 1995, Leibold 1999, Waide et al. 1999, Mittelbach et al. 2001) is likely to involve competition between animals within heterogeneous habitats (Kassen et al. 2000), but not relatively homogeneous such as in our study. This requires animals' competitive ability to vary between niches which in turn would require a trade-off between competitive and colonising ability which is rare in streams (Death 2002).

As predicted, between-stream richness increased monotonically with increasing productivity. The discrepancy in the productivity-diversity relationship found when assessing within- and between-stream scales in this study matches that commonly found between true local and regional scales (Currie 1991, Chase and Leibold 2002). Chase and Leibold (2002) found diversity peaked at intermediate levels of productivity at small scales and increased monotonically at the regional scale in pond communities. Several mechanisms have been put forward to explain the linear increase in richness at regional scales (Currie 1991, Waide et al. 1999, Mittelbach et al. 2001) and one likely factor is the inclusion of different niches as spatial scale increases (Kassen et al. 2000). Along with the regional linear increase in richness, Chase and Leibold (2002) found a monotonic increase in community dissimilarity with increasing productivity and more recently Chase (2010) suggested a greater deterministic control in low productivity environments. Many factors could explain this including increased resource heterogeneity and a greater number of stable states (Chase and Leibold 2002), but due to the nature of this experiment are not likely to apply. Accordingly, we found no relationship between community dissimilarity and productivity.

Dissimilarity increased with disturbance

Increasing disturbance led to greater dissimilarity between communities; this counters our prediction of greater deterministic control at higher disturbance (Chase 2003, 2007). Often differences in community dissimilarity can be explained by differences in the recolonisation process; i.e. deterministic and stochastic assembly patterns. Theory predicts β diversity should decline with environmental harshness due to a greater role of deterministic assembly (Chase 2007), such as that found when comparing spring and runoff-fed stream communities (Barquin and Death 2006). Nevertheless, recent work in lotic systems has demonstrated a greater deterministic control at intermediate levels of disturbance (Lepori and Malmqvist 2009) suggesting the transition from stochastic to deterministic control is not necessarily linear. Disturbance, especially in streams, typically operates at a patchy scale and creates heterogeneous habitat and resources (Doeg et al. 1989, Lancaster and Hildrew 1993). Thus, disturbance can promote diversity within a landscape (β and γ) by allowing both early colonising and

late successional species to coexist, but this is dependent on low dispersal (Warren 1996, Chase 2003, Chase and Ryberg 2004, Ostman et al. 2006, Matthiessen et al. 2010). Consequently, in natural systems we could have expected the increased dissimilarity with disturbance to be a result of increased resource/habitat heterogeneity. Due to the spatial and temporal scale of this experiment (dissimilarity assessed between equal disturbance treatments), disturbance was homogeneous between streams. Accordingly, resource heterogeneity (productivity variation) did not increase with disturbance rate nor did community dissimilarity with resource heterogeneity. In fact, resource heterogeneity is likely to be higher in more stable habitats at this scale (Beisel et al. 1998, Barquin and Death 2006).

Whether the increase in dissimilarity with disturbance is a result of greater stochastic assembly in more disturbed treatments is unclear (Chase 2003, 2007). A large proportion of New Zealand benthic invertebrates are capable of living in highly disturbed environments as a result of the high degree of environmental stochasticity and have generalist feeding habits as a result (Winterbourn et al. 1981, Thompson and Townsend 2000). In fact, there are many that could be considered 'Hutchinsonian demons' – both superior colonisers and competitors (Kneitel and Chase 2004, Cadotte et al. 2006). Essentially the role of deterministic assembly is less pronounced than in other ecosystems where harsh conditions select for few specialised taxa. In these streams, the proportion of taxa within the regional pool able to withstand these conditions is likely to be high.

Given the hypothesised lack of deterministic control in disturbed treatments, we suggest the increase in community dissimilarity with disturbance rate is simply a function of the time since last disturbance (Reice 1994). Considered this way, community dissimilarity declined with time, thus it appears these communities are converging on a single stable equilibrium. If β diversity is not promoted through different assembly processes (multiple stable equilibria), then heterogeneity in resources/conditions between streams (with single stable equilibria) would be required (Loreau and Mouquet 1999, Mouquet and Loreau 2002). Low connectivity between replicates as in this study (dispersal between streams), typically promotes multiple states (Warren 1996, Chase 2003, Chase and Ryberg 2004, Ostman et al.

2006, Matthiessen et al. 2010). Therefore, the convergence on a single stable equilibrium with time since disturbance between the streams indicates little heterogeneity between habitats and resources which was indeed evident in the present study.

Local suite of colonists

Rather than differences in assembly rules, it appears colonisation patterns are simply a function of the local suite of colonising taxa. Specifically, colonisation of channels appears to have come from the small-scale dispersal of animals present within the surrounding benthos of the spring-fed streams in which the study was undertaken; rather than a specialist suite of colonist taxa. Previous experiments of this nature have found this pattern of local arrival rather than the more broad-scale arrival of specialist colonisers (Death 2006). Thus the findings need to be considered with some caution as the colonisation patterns do not necessarily match those of large-scale natural disturbances. Communities found within the experimental channels, with a strong contribution of *Potamopyrgus antipodarum*, *Aoteapsyche colonica*, Platyhelminthes, Oligochaeta, *Deleatidium* spp. and *Pycnocentroides aeris* are similar to those found in the benthos in a previous study on these streams around this time (Tonkin and Death In prep.). If ecological theory holds, we would expect high disturbance treatments to be the most similar due to deterministic control selecting for few capable taxa but communities were more similar within streams than within disturbance treatments.

Our results suggest the increasing dissimilarity with disturbance rate was due to shifts in abundance of the most dominant taxa, although the mechanisms underlying this are unclear. The most abundant animal, the hydrobiid snail *P. antipodarum*, increased with disturbance rate which opposes research suggesting that this snail is inversely related to disturbance in streams (Holomuzki and Biggs 1999). Moreover, molluscs are generally considered slower colonisers and likely to be competitive dominants (Hemphill and Cooper 1983, Mackay 1992), but the atypical response to disturbance in this instance almost certainly reflects their abundance in the surrounding benthos. The response of *P. antipodarum* to disturbance has been found to be dependent on the type of substrate in the streambed (Holomuzki and Biggs

1999), but this is not likely a factor in the present study as substrates were relatively uniform between treatments. The decline of *P. antipodarum* with time since last disturbance may have been due to a competitive interaction with the hydropsychid caddisfly *A. colonica*. Disturbance can regulate the rate of competitive interactions between opportunistic early colonisers and competitive dominants which colonise slower (Hemphill and Cooper 1983). However, *A. colonica* did not necessarily replace *P. antipodarum* in this study, merely their relative abundances increased and decreased respectively. Although the negative interaction between these two species occurred within each stream, densities were clearly more site specific than disturbance specific. Nonetheless, where the substrate is regularly being turned over, it is likely to be unfavourable conditions for a net building caddisfly such as *A. colonica* which supports their increase with time since disturbance.

No suite of taxa were replaced with time since disturbance (Collier and Quinn 2003, Death 2006), but the negative association between *A. colonica* and *P. antipodarum* indicates a potential competitive-colonising trade-off. A critical requirement of many relationships in disturbance ecology is that there is a trade-off between competitive and colonising ability (Chesson and Huntly 1997, Roxburgh et al. 2004, Cadotte 2007). Neutral models have renewed debate on this central tenet in ecology (e.g. Hubbell 2001), but there is still widespread support for these trade-offs (e.g. Kneitel and Chase 2004, Cadotte et al. 2006). Previous studies looking at responses disturbance in streams indicate that rather than competitive displacement, original taxa remain and other taxa arrive with time but do not displace early colonisers (Death 1996, Collier and Quinn 2003, Death 2006). The expectation of no competitive displacement led us to predict a decline in richness with disturbance but we found no such pattern. Chase (2010) also found that taxa in low productivity habitats (harsh) were simply a nested subset of those found at higher productivities (benign), and argue that this is likely a more general pattern than previously thought. Indeed, the taxa found in high disturbance treatments in the present study are merely a subset of those found in stable treatments and although *P. antipodarum* declines with increasing stability, it is still dominant throughout all treatments. More

importantly, an underlying competitive interaction between *P. antipodarum* and *A. colonica* does not explain the increase in dissimilarity with disturbance.

Conclusions

Our results demonstrate that spatial scale can affect the way species diversity responds to environmental conditions. We have shown that diversity can respond to both productivity and disturbance but at different spatial scales. Specifically, taxonomic richness was lowest at intermediate levels of productivity at the within-stream (local) scale and increased monotonically at the between-stream (regional) scale. Rather than the increase in community dissimilarity previously found with increasing productivity (Chase and Leibold 2002) and the stronger role of deterministic assembly suggested for harsh environments (Chase 2007), we found an increase in dissimilarity with increasing rate of disturbance. Due to the abilities of the pool of colonists to withstand disturbed environments in these streams, communities are converging as a function of the time since last disturbance. Namely, they are simply returning to those found in the surrounding benthos as a result of the scale of disturbance and that it is not limiting the species pool. These patterns are highly dependent on the pool of colonists and are underpinned by interactions within each stream. Without a distinction between early colonising and late successional communities, increased deterministic assembly (and lowering of β diversity) with increasing disturbance will not apply. In fact, depending on the heterogeneity of regional habitats and connectivity between habitats, the opposite pattern may occur as we show here.

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Chapter 7

Synthesis



The aim of this thesis was to investigate the linkages between productivity, disturbance and diversity in stream macroinvertebrate communities and further the understanding of these relationships. I accomplished this by (i) assessing the application of diversity models such as the Dynamic Equilibrium Model (DEM) (Huston 1979, 1994, Kondoh 2001) and a more contemporary stream-specific productivity-disturbance-diversity model (Death 2002), as well as developing and testing a multivariate model of diversity based on observed patterns in New Zealand mountain streams; and (ii) exploring the form these links in further detail between New Zealand and Spanish streams as well as investigating the underlying mechanisms driving these relationships in lotic systems. The prevailing premise is that diversity increases with increasing productivity and declines with increasing disturbance, although there was slight variation in the form of these relationships between chapters.

The strength of the link between productivity, disturbance and diversity of stream macroinvertebrate communities was clearly demonstrated in this study. Firstly, a large scale study of mountain streams indicated that productivity and disturbance could both independently predict diversity but the relationship was affected by the presence of canopy cover, in that strong links were present in open canopy streams but not those with canopy cover (Chapter 2). However, this relationship was consistent between regions of differing land use (Chapter 3). Secondly, I demonstrate that where productivity-diversity relationships are not obvious, invertebrate communities may be controlled by the growth form of the periphyton community rather than its biomass (Chapter 4), or may simply be a function of the range of productivity considered (Chapter 5). In fact, global productivity-diversity relationships may exist in streams, even where individual differences in the shape of the curve between regions are evident. Finally, there is a strong effect of the spatial scale of consideration in productivity-diversity and disturbance-diversity relationships (Chapter 6).

One of the more important hypotheses I tested was whether productivity and disturbance interact to modulate diversity (Kneitel and Chase 2004, Scholes et al. 2005, Cardinale et al. 2006), or whether they operate independently. Because the link between productivity and disturbance in streams is particularly strong (Lake 2000,

Death 2002, Cardinale et al. 2006), they are thought to interact to generate outcomes on diversity. This interactive effect is a central component of the DEM, but although both productivity and disturbance could predict diversity at individual scales, there was no evidence of a statistical interaction between the two (Chapter 2 and 3). That is, the effects of productivity and disturbance were additive, rather than multiplicative at individual scales.

In Chapter 2 I found some support for the Intermediate Disturbance Hypothesis (IDH) (Grime 1973, Connell 1978, Sousa 1979), with a unimodal relationship between disturbance and diversity. However, a second study assessing this relationship suggested diversity declined with disturbance and this was consistent between two regions of contrasting land use intensity (Chapter 3). Despite finding support for the IDH in Chapter 2, the relationship between productivity and diversity did not match that of the DEM, exhibiting a log-linear increase in diversity with increasing productivity. This increase matches the assertion of Death (2002) that productivity sets the upper limit to richness in stream communities rather than leading to a greater rate of competitive interactions. Death (2002) further suggests the role of disturbance is to simply remove taxa and reset colonisation, allowing for productivity to set maximum richness. Therefore, I developed a model, building on Death's model, which predicts that diversity is a unimodal/quadratic function of disturbance, with productivity determining the magnitude of that peak.

This model, and that of Death (2002), were similar in their predictive ability in both a pristine region and a region more heavily impacted by land use change (Chapter 3). However, this suggested a quadratic decline rather than the unimodal trend found in Chapter 2. The link between productivity, disturbance and diversity did not differ between these regions, which is interesting considering the contrast in anthropogenic influences in each region's environment. When assessing whether the productivity-disturbance-diversity relationship differed between streams with or without canopy cover, I found it was only evident at open canopy sites. This was not a result of the correlation between canopy cover and stream size and it remains unclear as to what the main determinant of diversity in sites with canopy cover is. However, the difference in productivity-disturbance-diversity links between sites with and without

canopy is likely to be related to a stronger coupling between invertebrate communities and algal productivity in autotrophic than heterotrophic streams. The relationships between productivity, disturbance and diversity can be highly variable with the spatial scale at which they are assessed (Petraitis et al. 1989, Currie 1991, Mackey and Currie 2001, Chase and Leibold 2002) as I have shown in experimental stream channels (Chapter 6), and altering productivity or disturbance can lead to changes in assembly sequences of animals. Interestingly, this experiment indicated that either productivity or disturbance individually affected diversity at each scale. This differs from the findings in Chapters 2 and 3 where, although operating independently, productivity and disturbance both had strong influences on diversity at the same scale of assessment.

Given that productivity-diversity relationships are a relatively little studied area of lotic ecology, I was interested in whether productivity set the upper limit to richness in streams elsewhere in the world (Death 2002, Barquin 2004), or whether greater productivity led to competitive exclusion. Although the effects of productivity on diversity were strong in all the New Zealand streams, there was no direct relationship in the 24 Spanish streams assessed (Chapter 4 and 5).

While measuring primary productivity indicates the rate of production of energy, it does not account for the specific form of plants driving this production. Assessing the response of macroinvertebrate diversity to two coarse measures of periphyton community composition found strong responses where a simple measure of primary productivity (chlorophyll *a*) could not (Chapter 4). Specifically, macroinvertebrate diversity tended to be negatively associated with filamentous algal forms and positively associated with periphytic mats. Moreover, when testing the response of these streams along the same axis as 24 New Zealand streams (Chapter 5), they were simply a continuation of a log-linear curve found in the New Zealand streams, suggesting this may be a universal pattern. Despite the wide range of productivities assessed, there was no evidence for a decline in diversity at greater rates of productivity which suggests competitive exclusion is not occurring as is required for the DEM to apply.

The overwhelming evidence found in this thesis is that productivity simply increases diversity, with no evidence of an increase in competitive interactions at greater levels of productivity. The log-linear link between productivity and diversity was not limited to New Zealand streams with a universal pattern emerging between the Spanish and New Zealand streams. Furthermore, I provide reasons for a lack of obvious link between productivity and diversity including underlying biotic interactions and the scale at which the relationship is assessed. Disturbance, on the other hand, exhibited more variable effects on diversity, although the prevailing theme is that disturbance simply removes taxa at a variable rate. This thesis goes a long way towards identifying the true form of both the productivity-diversity and disturbance-diversity relationships in streams. I provide further evidence to suggest the DEM is not applicable in stream systems, which is likely due to a lack of competitive exclusion. Finally, although the effects of productivity and disturbance are strong, I propose that they do not interact to affect diversity in stream macroinvertebrate communities but operate independently.

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Appendix 1: Raw invertebrate data collected from 47 streams (Chapter 2) in the Tongariro National Park, New Zealand, between February and April 2007. Values are mean number of individuals collected from five Surber samples (area = 0.1 m²) at each site. Site names are given in Appendix 2.

No.	Taxon	1	2	3	4	5	6	7	8
Ephemeroptera									
1	<i>Deleatidium</i> spp.	56	43.6	71.2	80	17.4	23.8	51.6	28
2	<i>Nesameletus ornatus</i>	0	0.4	0.2	0	0	0	0	0
3	<i>Coloburiscus humeralis</i>	3.2	1.2	24.4	18.8	0.4	5.4	47	7.6
4	<i>Acanthophlebia cruenata</i>	0	0	0	0.2	0	0	0	0
5	<i>Austroclima sepia</i>	0	0	2.4	2.4	1.6	0.2	5.2	3
6	<i>Austroclima jollyae</i>	0	0.8	0	0	0	0.4	4	1
7	<i>Maiulus luma</i>	0	0	0	0	0	0	0	0
8	<i>Zephlebia spectabilis</i>	0	0	0	0	0	0	0	0
9	<i>Zephlebia borealis</i>	0	0	0	0	0	0	0.6	0
10	<i>Zephlebia versicolor</i>	0	0	0	0	0	0	0	0
11	<i>Zephlebia dentata</i>	0	0	0	0	0	0	0	0
12	<i>Zephlebia tuberculata</i>	0	0.4	0	0	0	0	0	0
13	<i>Amelotopsis perscitus</i>	0	0	0	0	0.2	0	0	0
14	<i>Neozephlebia scita</i>	0	0	0	0	0	0	0.4	0
Plecoptera									
15	<i>Zealandoperla</i> spp.	22.4	30.2	52.8	116	0.8	1	41.4	4.8
16	<i>Zealandobius confusus</i> gp.	0	0	0	0	0.2	0.2	0	0.4
17	<i>Zealandobius furcillatus</i> gp.	0	0	0	0	0	0	0	0
18	<i>Austroperla cyrene</i>	1.2	0.6	3.8	4	0	2.8	3	0.6
19	<i>Stenoperla prasina</i>	0	0.6	0.4	0.6	0	0	0	0
20	<i>Taraperla pseudocyrene</i>	0.2	0.2	0	0	0	0	0	0
21	<i>Megaleptoperla diminuta</i>	0	0	0	0	10.2	0	0	0
22	<i>Megaleptoperla grandis</i>	1.8	2.8	5.2	6.6	0	4.2	10	9.8
Trichoptera									
23	<i>Aoteapsyche colonica</i>	0	1.4	9.2	16	0	3.4	55	0
24	<i>Orthopsyche fimbriata</i>	0.2	0	0	0	0	0	0	0
25	<i>Orthopsyche thomasi</i>	0.8	0	0	0	0	0	0.4	2.4
26	Early instar Hydrobiosidae	1.4	0.4	1.6	4	4.8	0	1.4	0
27	<i>Psilochorema</i> A	0.2	0.4	0.8	0	4.2	0.2	0.2	0
28	<i>Hydrobiosis parumbripennis</i>	0.2	0.2	1.2	0	1.6	0.2	0.2	1
29	<i>Hydrobiosis silvicola</i>	0	0	0	0	0	0	0	0
30	<i>Hydrobiosis frater</i>	0	0	0	0	0.4	0	0	0
31	<i>Hydrobiosis spatulata</i>	0.2	0	0	0	0	0	0	0
32	<i>Hydrobiosis clavigera</i>	0	0	0	0	0	0	0	0
33	<i>Hydrobiosis charadrea</i>	0	0	0	0	0	0	0	0
34	<i>Neurochorema forsteri</i>	0	0.2	0	0	0	0	0.4	0
35	<i>Neurochorema confusum</i>	0	0	0	0	0	0	0	0.2
36	<i>Costachorema callistum</i>	0	0	0.2	0	0	0	1	0.6
37	<i>Costachorema xanthopterum</i>	0	0	0	0	0	0	0.2	0

No.	9	11	12	13	14	15	16	17	18	19	20	21
1	3.6	2.8	16.4	52.2	143.6	72.6	145.6	106.4	9.6	38.4	29.6	16.8
2	0	0	0	0	0	0	0	4.2	0.8	3	2.6	1
3	0	0	1	0.4	0	4.8	12.8	9.4	46.4	1	4.8	0.2
4	0	0	0	0.8	0	0	1	0	0	0	0	0
5	0	0	2.4	0.2	0.4	0.2	0	1.2	101.6	2.4	1.6	0.8
6	0	0.8	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0
10	0.8	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	2	0	0
12	0	0	0	0	0	0	0	0	0	0	0.2	0
13	0	0	0	0.2	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0.2	0	0.8	0	0	0
15	3.4	14.8	15.6	14.8	12.4	25.8	42.4	19.6	8	10.4	18.6	73.2
16	0.6	0	0.8	0.8	23.2	0.2	0	0.4	0	2	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0
18	0.4	0	0.2	0.8	7	11.8	0	11.6	10.6	0.8	0.8	0.8
19	0	0	0.4	0.4	1	0.2	1.8	0.8	0	1	0.8	0
20	0	0	0	0	0.4	0	0	0	4	0.6	0	0
21	0	0	0	0	0	0.2	0	0	0	0	0	0
22	1.2	0	24.2	2	21.2	4.2	0	5.2	0	0.8	1.2	0.8
23	29.6	16.2	0	0.2	0.4	1.4	11.2	9.6	20.8	1.8	0	5.6
24	0	0	0	0	0	0	0	0	0	0	2.4	0
25	0	0	0.8	0	0	0	0	0.2	0	0	0	0
26	0.8	0.8	0	4.4	2.8	0.4	3.2	1.6	12.8	0	7.2	6.6
27	0	0	0	0.2	2.4	0	4	2.4	4.8	5	2.6	0.8
28	1.2	0	2.4	0.2	0	0.4	0	1.6	16	0.6	1.8	2.8
29	0	0	0	0	0.2	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0.8	0	0	0
32	0	0	0	0	0	0	0	0.2	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0
34	0.8	0	0	1.2	0	0	0	0	0.8	0	0.6	1
35	0	0	0	0	0	0	0	0	0	0	0	0
36	1.8	0.4	0.8	0	0.6	0	0.2	0	0.8	0	1.6	0.8
37	0	0	0	0	0	0	0	0	0	0	0	0

No.	22	23	24	25	26	27	28	29	30	32	33	34
1	113.6	69.2	8.2	50.8	83.2	52.8	34.8	87.4	4.6	0	5.6	56
2	8	7.4	1.8	0.4	0	0	13.4	0	0	0	0	0
3	8.8	23	0	3.2	0	1	0	0	0	0	0	0
4	0	0.4	0	0	0	0	0	0	0	0	0	0
5	67.2	11.2	0.8	3.4	0.4	0	0	0	0	0	0	2.4
6	0	1	0	0	0	2.4	3.4	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0
8	0	12.8	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0
11	0	7.2	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0.2	0	0	0	0	0	0	0	0	0	0
14	0	3.2	0	0	0	0	0	0	0	0	0	0
15	7.2	2.2	51.8	51	21.8	39.2	47.8	0	14.4	0.6	42.6	81.6
16	0	0.4	0	0	0	0	0.2	2.8	0	0	1	2.2
17	0	0	0	0	0	0	0	0	0	0	0	0
18	8	0.8	0	0.2	0	0.2	0	1.8	0	0	0.2	5.6
19	0	0.2	0	0	0	0	0	0	0	0	0	0
20	2.4	0	0	0	0	0	0	0	1.6	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0
22	7.2	0.8	0	0	0.8	1.8	0.2	1.6	0	0	0.6	1.8
23	0.8	0.8	13.8	98.2	21.4	9	3.8	0	0	0	19.8	4
24	0	0	0	0	0	0	0	0	0	0	0	0.2
25	0	0	0	0	0	0	0	0	0	0	0	0
26	2.4	0	5.6	2.4	3	5.2	0.6	0	1	0.2	0.6	5
27	2.4	4.6	0	0.8	0.2	0	0	0	0.8	0	0	1
28	4	0.8	0.8	1.6	5.6	2.2	0.4	33	1.6	0	0.2	1.4
29	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0.2	0
32	0	0	0	0	0	0	0	0	3.4	0	0	0
33	0	0	0	0	0	0	0.2	0	0	0	0	0
34	0	0	0.8	0.2	1.8	0.2	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0
36	3.2	0	2.4	0	1.2	0	0.2	0	0	0	0	2.4
37	0	0	0	0.4	0	0	0	0	0	0	0	0.2

No.	35	36	37	38	39	40	41	42	43	44	45	46
1	76.8	153.6	15.8	8.4	49.8	15	25.2	32.8	72.8	73.2	7.4	6.4
2	0	0	0	0	0	0	0	0	0.2	4.8	0.2	0
3	13.6	24.8	0	0	20	0.8	1.2	14.6	22.8	22.6	1.6	0
4	0	0	0	0	0.2	0	0	0	0	0	0	0
5	116	37.6	1	0	1	1.4	0	62.4	9.4	3.2	12.2	0
6	0	0	0	0	1.8	0	11	0	0	0	0	0
7	0	0	0	0	2.2	0	0	0	0.2	0	0	0
8	0	0	0	0	0	0	0	0	0	1	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0
11	8	0	0	0	0	0	0	0	0	0	4.8	0
12	0	0	0	0	0	0	0	1.6	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0.2	0.2	0
15	0	35.2	8.4	19.4	18.4	29.4	7.6	21.6	14.2	44.2	0	19.6
16	150.4	20	2	4.4	0.8	12.6	0	4	19.2	1.8	2.4	0
17	0	0	0	0	0	0	1.6	0	3.6	0	0	0
18	13.6	0	0	0	1.6	0	3	2.4	7	3.8	1	0
19	0	0	0	0	1.4	0.2	0	0	1.8	0	1.6	0
20	0.8	0	0	0	0	0	0	3.4	0	0.2	0	0
21	0	0	1	0	0	0	0	0	0	0	0	0
22	14.4	3.2	0	2.2	0.6	0.2	0.8	0.8	1.8	0	0	0
23	0	0	0.4	1	2.2	6.2	13.6	0	0	2	0	1.8
24	32.8	0	0	0.4	0.4	0	1.6	23.4	30.6	0	6.8	0
25	0	12	0	0	0	0	0.8	0	0	0	0	0
26	8.8	2.4	0.2	1	3.2	3.2	7.8	4.8	14.2	2.4	0	0.6
27	0	0	0	0	0.4	0	0.8	0	1	3.8	1.4	0
28	7.2	0.8	0.4	2	6.2	1.4	3.4	0.2	2	1	0	0
29	0	0	0	0	0	0	0	0	0.6	0.2	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	1.4	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0.4	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0
34	3.2	0.2	0	0	1.2	3.2	1.8	0	0.8	0.2	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0.4	1.4	0	2	1.6	3	1.2	0	0
37	0	0	0.2	0	1.2	0	0	0	0	0	0	0

No.	47	48	49
1	42.4	13.8	102.2
2	0	0.2	0
3	0	0	0
4	0	0	0
5	0	0.2	1
6	0	0	0
7	0	0	0
8	0	0	0
9	0	0	0
10	0	0	0
11	0	0	0
12	0	0	0
13	0	0	0.2
14	0	0	0
15	31.2	38	13.4
16	0.4	0	0
17	0	0	0
18	0.6	0.2	0.8
19	0.2	0	0
20	0	0	0
21	0.2	0	0.8
22	0	0	0
23	4.8	15.4	1
24	0	0	0
25	0	0	0
26	1.8	4	3.6
27	1	0.4	0
28	0	0	0.8
29	0	0	0
30	0	0	0
31	0	0	0
32	0	0	0
33	0	0	0
34	0	0	2.4
35	0	0	0
36	0.4	0	0.2
37	0	0.2	0

No.	Taxon	1	2	3	4	5	6	7	8
38	<i>Costachorema psaropteron</i>	0	0	0	0	0	0	0	0
39	<i>Hydrobiosella mixta</i>	0.2	0	0	0	0	0	0	0
40	<i>Hydrochorema crassicaudatum</i>	0	0	0	0	0	0	0	0
41	<i>Pycnocentria evecta</i>	0	0.2	1.2	1.6	0	0.2	5.6	0
42	<i>Pycnocentria funerea</i>	0.2	0	0	0	0	0	1.6	0.6
43	<i>Pycnocentria sylvestris</i>	0	0	0	0	0	0	0	0
44	<i>Pycnocentrella eruensis</i>	0	0	0	0	0	0	0	0
45	<i>Pycnocentroides aeris</i>	0	6.8	9.2	0	0	0.2	43.6	0.4
46	<i>Beraeoptera roria</i>	2.2	48.4	75.2	24.8	0	5.2	154.4	34.4
47	<i>Confluens hamiltoni</i>	0	2.4	0	0.2	0	0	2	0.4
48	<i>Oeconesus similis</i>	0	0	0	0	0	0	0	0
49	<i>Oecetis</i> sp.	0	0	0	0	0	0	0	0
50	<i>Hudsonema amabile</i>	0	0	0	0	0	0.2	0	0
51	<i>Hudsonema alienum</i>	0	0	0	0	0	0	0	0
52	<i>Oxyethira albiceps</i>	1.2	0	3.6	0.8	0	0	2.8	0
53	<i>Paroxyethira hintoni</i>	0	0	0	0	0	0	0	0
54	<i>Olinga feredayi</i>	0	4.8	3.4	8	0	0.6	4	1
55	<i>Helicopsyche poutini</i>	0	1.8	1.4	7.2	0.4	0	1	0.4
56	<i>Zelolessica cheira</i>	0.8	0	0	0	3.2	0	0	4.8
57	<i>Allocentrella</i> sp.	0	0	0	0	0	0	0	0
58	Caddis Pupae	0	0	0	0	0	0	0.6	0
59	<i>Polyplectropus</i> sp.	0	0	0	0	0	0	0	0
60	<i>Philorheithrus agilis</i>	0	0	0	0	0	0	0	0
	Diptera								
61	Orthoclaadiinae A	0	0	0	0.8	0	0	0	0.4
62	Orthoclaadiinae B	0.2	0	1.2	4	0.6	1.2	0.6	0
63	Orthoclaadiinae C	2.4	0	0	7.2	3	1	25.6	0
64	Orthoclaadiinae D	4.2	1	0	0	0	0	0	0
65	Orthoclaadiinae E	8.4	1.8	0.2	0	84.6	0.4	19	3.2
66	Orthoclaadiinae F	0	0	0	0	1	0	0	0
67	Chironominae A	35.8	0.4	0	0	6.2	0.2	1.4	0.8
68	<i>Maoridiamesa</i> sp.	68.2	13	0.2	7.2	0.8	0.2	16.8	2.6
69	Tanypodinae A	0	0	0	0	0	0.2	0.2	0
70	Chironomidae pupae	7.4	0.2	0	0	4	0.2	2.8	0
71	Eriopterini (other)	1	0.8	0.6	1.6	2.8	3.2	0.4	1
72	<i>Molophilus</i> sp.	0.2	0	0	0	0	0	0	0
73	<i>Aphrophila neozelandica</i>	4	2	6.8	5	0	2.6	20.6	0
74	<i>Austrosimulium</i> spp.	0	0	1	1.6	3.6	0	0.4	0
75	<i>Mischoderus</i> sp.	0.2	0	0	0	0.2	0	0	0
76	Empididae	0.6	0	2	0	0.8	0	0.6	0
77	<i>Limonia</i> sp.	0	0	0	0	0	0	0	0
78	<i>Neocurupira hudsoni</i> gp.	0	0	0	0	0	1.2	0	0
79	<i>Paradixa</i> sp.	0	0	0	0	0	0	0	0

No.	9	11	12	13	14	15	16	17	18	19	20	21
38	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0.2	0	0.2	0	0	0.4	0	0
40	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	24.8	0.2	0.2	0
42	0	0	0	0.4	0.2	0	0	0	0	9.2	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0
45	0.8	0	6.4	0	0	0	0	0.4	4	0	0	0
46	0	0	0.2	6.4	0.2	35	16.8	18	0.8	0.2	0.8	1.6
47	0.2	0	0	0	0	0	0	0	36.8	0.6	0	1.6
48	0	0	0	0	0.2	0	0	0	0	4.2	0	0
49	0	0	0	0	0	0	0	0	0	2.8	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	1	0	3.6	0	0	0	1.6	0	1.6	0.8
53	0	0	0	0	0	0	0	0	0	0.2	0.8	0
54	0.4	0	1.4	1.8	0	6.4	7.2	3.2	0	0.2	4.8	1.6
55	0	0	0.8	0	0	21.6	0.8	5.6	0	6.8	0	0
56	2.6	0	4.2	1.4	1.8	0	0	0	76	0.6	0	0
57	0	0	0	0	0	0	0	0	24	0.2	0	0
58	0	0	0	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0.4	0.2	0
60	0	0	0	0	0	0	0	0	0	0	0	0
61	0	0	0	0	0.4	0	7.2	0.8	0	4.4	0	0
62	10.4	5.6	6	25.2	7.6	1.6	0.8	0.8	8.8	2.6	0	0
63	6.8	0	1.6	10	0	0	0.8	0	5.6	2.2	541.6	170.8
64	0	0	0	9.2	16.6	0	0	0	0	0	0	0
65	11.6	2	0	34	33	3.2	0	2	72.8	12.6	57.6	67.6
66	0	0	0	0	0.4	0	0	0	0	0	4	0
67	10.4	1.6	8	5	35.4	0	0	0.8	0.8	0	0.8	0
68	82	2.6	87	11.8	4.8	0	0	0	6.4	0.8	132	81.2
69	0	0	0	0	0	0	0	0	0	0.2	0	0
70	0	0	1	0.4	6.2	0	0	0	1.6	0	16.8	9.2
71	0	2.2	0	1.2	2.6	2.6	0	0.8	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0
73	0.6	1.2	9.2	5.4	5.4	2.4	7.2	6.6	8	0	0.8	1.6
74	0	2.4	2.4	0	0	0	0	0	4	0	1.6	0
75	0	0	0	0	0	0	0	0	0	0	0	0
76	0.2	1.4	8.4	0	0.2	0	0	0.8	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0.8	0
78	0	0	0	0	0	1.8	0	0	0	0	0	0.2
79	0	0	0	0	0	0	0	0	0	0.4	1.6	0

No.	22	23	24	25	26	27	28	29	30	32	33	34
38	0	0	0	0	0	0	0	0	0	0	0	0
39	0	1.6	0	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0.2	0	0	0	0	0	0	0	0
42	9.6	5.2	0	0	0	1.6	0	0	0	0	0	1.8
43	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0
45	30.4	10.8	0	0	0.4	13.6	1.4	0	1.6	0	0.2	0.8
46	6.4	0	6.2	29	2.6	29.6	0.6	0	0	0	6.6	2.4
47	0	0	2.4	0	27.8	10.4	0	0	0	0	0	6.4
48	0	0	0	0	0	0	0	0	0.2	0	0.2	0
49	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	0	0
52	4	0	11.4	0.2	1	0.4	0	0	0.8	0	0.4	0
53	0	0	0	0	0	0	0	0	0	0	0	0
54	0	1.8	0	1	0	0	0	0	0	0	0	0
55	2.4	43.6	0	0	0	0	0	0	0	0	0	0
56	0.8	0	0	0	0.4	0	0.6	181.4	7.2	0.2	0.2	1.6
57	0	0.8	0	0	0	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0	0.4	0
59	0	0	0	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0
61	0	2.4	0	0	0	1.6	0.2	0	0	0.2	0	0
62	0	0.8	15.2	0	0	29.6	1.2	157.4	103.2	2	6.2	4.2
63	0	0.8	133.6	3.6	0	17.6	1.8	0.4	8	0	1.6	2.6
64	0	0	16.8	0	57	4.8	0	0	0	0	0.6	1.2
65	23.2	0	41.6	2	0	16.8	0	0	20	0	6.2	1.6
66	0	0	0	0	0	0	0.2	0	0	0	0	0
67	2.4	0	0	0	0	3.2	0.4	0.4	0	0	0	0
68	16.8	0.8	535.2	15.6	20.2	92	0.2	692.8	189.6	0	19	0.6
69	0	0.8	0	0.2	0	0	0	0	0.2	0	0	0
70	0	0	5.6	0.2	1.8	0.8	0.2	9.4	2.4	0.6	0.4	0.4
71	2.4	0	0	1.6	0.6	0.2	1.4	0	0	0	0.8	4
72	0	0	0	0	0	0	0	0	0	0	0	0
73	2.4	1	1.6	6.4	18.2	14.4	3	0	0	0	0	3.6
74	3.2	0	2.4	0	0	0.8	2	0	1.6	0	4.6	1.2
75	0	0	0	0	0	0	0	0.2	0	0	0.2	0
76	0	0	0	0	0	0	0	20	0.8	0	0	0.8
77	0	0	0	0	0	0	0	0	0.8	0	0	0
78	0	0	0	0	0	0	0	0	0	0	0	0
79	0	0.8	0	0	0	0	0	0	0	0	0	0

No.	35	36	37	38	39	40	41	42	43	44	45	46
38	0	0	0	0	0.8	0	0	0	0	0	0	0
39	0.8	0	0	0	0	0	0	0	0	0	0.8	0
40	0.2	0	0.2	0	0.2	0	0	0.4	0.2	0	1	0
41	28	0	2.4	0	0.6	0.6	18.8	0	0	0	0	0
42	0	4	0	0	0	0.6	17	22.4	3.8	0.2	0	0
43	0	0	1	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	1.6	0
45	0	0	11.2	2	0.2	0.2	8.6	0	0	0	0	0
46	0	0.8	14.6	2.2	7.8	0.8	1.2	0	0	30.4	0	0
47	0	0	0	0	7.4	0	5	0	0	0.4	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0.2	0	0	0.2	0	0
52	1.6	0.8	0	0	0.4	0	0	0	0.2	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0.4	0.2	0	0	0	1	0	0
55	10.4	0	0	0	0	0	0.8	3.2	0.6	22.6	7.6	0
56	19.2	1.6	25	0.2	15.2	0	27	12.8	2.2	0	0	0
57	8	0	0	0	0	0	0.8	2.4	0	0	2	0
58	0	0	0	0	0	0.4	0	0	0.2	0	0	0
59	0	0	0	0	0.2	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0.2	0
61	0	0	0	0	1	0	0.2	0.8	0	0	1.2	0
62	0	0	34	38	58.8	39.2	3	4	27.8	5.4	0	0
63	7.2	4	1.6	0	18	11	0	1.6	0	0	0	0
64	0	0	0	0	4.2	1.8	0	0	9.6	0	0	0
65	32	3.2	12.4	2.2	0	3.8	2.4	4	0	0	0.6	0
66	0	0	0	0	0	0	0	0	0	0	0	0
67	6.4	0	0	0	1.2	4	0	0.8	0.2	0	0	0
68	20.8	4	29.4	50.2	4.2	37	20.6	0	0	0.8	0	0
69	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0.8	3.6	0	6.8	3.6	0.8	0	1.4	0.4	0	0
71	0.2	0.8	0.2	0.6	2	4.4	0	0	1.6	0.4	0.2	1.4
72	0	0	0	0	0	0	0	1.6	0	0	0	0
73	6.4	0	0	0	20.2	2.4	1.6	0	3.6	5.8	0	0
74	4	0	0.8	1.4	0	0.6	0	3.2	1	0	0	0
75	0	0	0	0	0.6	0	0	0	0	0	0	0
76	0	0	0	0	0.4	0	0.4	0	0	0	0	0
77	0	0.8	0.4	0	0	0	1	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	0	0	0
79	0	0	0	0	0	0	0	0	0	0	0	0

No.	47	48	49
38	0	0	0
39	0	0	0
40	0.2	0	0
41	0	0	0
42	0	0	0
43	0	0	0
44	0	0	0
45	0	0	0.8
46	0	0	0.2
47	0	0	0
48	0	0	0
49	0	0	0
50	0	0	0
51	0	0	0
52	0.4	0	0.8
53	0	0	0
54	0.6	0	0.8
55	0	0	0
56	0	0	0.8
57	0	0	0
58	0	0	0
59	0	0	0
60	0	0	0
61	0	0	0
62	9	8	27.4
63	4.8	25.2	74.8
64	0	0	10.4
65	0.4	1	0
66	0	0	0
67	0	0.4	5
68	3	1.2	7.8
69	0	0	0.8
70	3.2	1	2
71	3.2	0.6	6.2
72	0	0	0
73	0.2	0.4	7.4
74	1.8	2.8	0.8
75	0	0	0
76	0	0	1
77	0	0	0
78	0	0	0
79	0	0	0

No.	Taxon	1	2	3	4	5	6	7	8
80	<i>Nothodixa</i> sp.	0	0	0.2	0	0.4	0	0	0
81	<i>Ephydrella thermarum</i>	0	0	0	0	0	0	0	0
82	Ceratopogonidae	0	0	0	0	0	0	0	0
83	Muscidae	0	0.8	0	0	0.8	0	0	0
Coleoptera									
84	Elmidae <i>Hydora</i> spp.	9.2	13.6	24	20	0	2.4	2.6	12.4
85	Hydraenidae	0	2	2.4	0.8	1	0	1.4	0
86	Ptilodactylidae	0	0	0.2	0	0.2	0	0	0
87	Hydrophylidae	0	0.2	0	0	0.2	0	0	0
88	Scirtidae	0	0	0	0	0	0	0	0
Mollusca									
89	<i>Potamopyrgus antipodarum</i>	0	0	0	0.8	0	0	0.6	0
90	<i>Latia neritoides</i>	0	0	0	0	0	0	0	0
91	<i>Gyraulus corinna</i>	0	0	0	0	0	0	0	0
Other									
92	<i>Archichaulioides diversus</i>	0	1	2.2	1.6	0.6	1.4	4.4	1.4
93	Platyhelminthes	0	0	0	0	0	0	0.4	0
94	Oligochaeta	1.8	0	2.8	2.4	27.2	0.2	0.4	0
95	Neuroptera <i>Kempynus</i> spp.	0	0	0	0	0	0	0	0
96	Nematoda	0	0.2	0	0	0	0	0	0
97	Ostracoda	0	0	0	0	0	0	0	0
98	<i>Paricalliope</i> spp.	0	0	0	0	0	0	0	0
99	<i>Anisops assimilis</i>	0	0	0	0	0	0	0	0
100	Nematomorpha	0	0	0	0	0.2	0	0	0

No.	9	11	12	13	14	15	16	17	18	19	20	21
80	0	0	0	0	0	0	0	0	0	0	0	0
81	0	0	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	2.4	0	0	0
83	1	0	0	1.4	0	0	0	0	0.8	0	0.2	3.4
84	8.8	0	0.8	22	9.8	30.4	5.6	10	46	0.6	7.2	5
85	0	0	0	1.6	6	1.6	0.8	2.6	30.4	1.6	2.4	0
86	0	0	0	0	0.2	0	0	0	3.2	0.2	0	0
87	0	0	0	0	0	0	0	0.8	0.8	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0.2	0	0	0	0	0	0	0.4	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	2.6	0.4	1.6	4.8	0.4	4	0	1.6	0.8
93	0	0	1	0	0	0	0	0	1.6	0.8	0	0
94	0	0.2	0.8	1	1.2	0	19.2	5.6	9.6	21.2	4	2
95	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0.2	0	0	0	0	0	0.4	0	0
97	0	0	2.4	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0	0	0	0	0	0
100	0.2	0	0	0	0	0	0	0	0	0	0	0

No.	22	23	24	25	26	27	28	29	30	32	33	34
80	0	0	0	0	0	0	0	0	0	0	0	0
81	0	0	0.2	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	3	0.8	0.8	9.6	0.2	2	16.6	0	0	0
84	80	8.8	2.4	15.6	24.4	20.8	20	6.8	12.8	0	2.8	22.8
85	16	5.2	0	0.8	0	0	0	0	0	0	0	0.4
86	1	0	0	0	0	0	0	0	0	0	0	0.8
87	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0.2	0	0	0
89	0	4.6	0	0	0	0	0	0.2	0.8	0	0	0
90	0	6.6	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0
92	1.6	3.4	0	0	0	0	0	0	0	0	0	1.6
93	6.4	4.4	0	0	0	0	0.4	6.4	0	0	0.4	0
94	17.6	1.8	12	4	1.6	0.8	0	1	59.2	0	0	5.8
95	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0.4	0.8	0	0	0	0	0	0.8	0	0	0
97	0	0	0	0	0	0.8	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0	0	0.2	0	0	0
100	0	0	0	0	0	0	0	0	0	0	0	0

No.	35	36	37	38	39	40	41	42	43	44	45	46
80	0	0	0	0	0	0	0	0	0	0	0.2	0
81	0	0	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0.4	0.2	0.6	1.2	3	0	0	0	0	0
84	28	120	0.2	0	10.6	11.4	34.4	1.6	37	4.4	0	1.2
85	22.4	0.8	0	0	0.2	0	0.8	0	3.8	7.8	0	0
86	14.4	0	0	0	0	0	1	6.4	1.4	0	0.2	0
87	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0.8	0	0	0
89	8	0	0	0	0	0	0	0	0	0.6	0.6	0
90	0	0	0	0	0	0	0	0	0	0	0	0
91	0.2	0	0	0	0	0	0	0	0	0	0	0
92	0	4.2	0	0	4	0	5.4	0	0.6	6	0	0
93	7.2	0	1.8	1.6	0.2	0	4	2	0	0.4	2.4	0
94	14.4	6.4	25	1.6	23.2	4.8	16.2	3.2	3	1.2	0.2	0.2
95	0	0	0	0	0	0	0	0	0	0.2	0	0
96	0	0	0.6	0.6	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0.8	0	0	14.8	0
99	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0.4	0	0	0	0	0	0	0

No.	47	48	49
80	0	0	0
81	0	0	0
82	0	0	0
83	0	0	0.8
84	4.2	2.4	20.6
85	1	0	0
86	0	0	0
87	0	0	0
88	0	0	0
89	0	0	0
90	0	0	0
91	0	0	0
92	0	0	0
93	0	0	0
94	0.4	3.8	0
95	0	0	0
96	0	0	0
97	0	0	0
98	0	0	0
99	0	0	0
100	0	0	0

Appendix 2: Sampling location information for the 47 streams used in Chapter 2 in the Tongariro National Park, New Zealand, sampled between February and April 2007. Altitude = m asl. * Indicates the 24 New Zealand sites used in Chapter 5.

Site no.	Site name	Easting	Northing	Altitude
1	Te Whaiiau stream	2735629	6236670	643
2*	Whanganui @ Te Porere	2734447	6236741	654
3*	Whanganui d/s intake	2735280	6239631	604
4*	Mangatepopo by camp	2731856	6234203	752
5	Rotoaira trib	2745962	6232119	570
6	Mangahouhounui	2751536	6231933	540
7*	Poutu Stream	2752035	6232647	518
8	Puketerata SH1	2752750	6228950	590
9*	Oturere Stream SH1	2748265	6221043	809
11*	Mangatoetoenui @ SH1	2745841	6215290	971
12*	Unnamed @ SH1	2748253	6219911	885
13	Waihaha stream	2752693	6222742	651
14	Trib of Mangawhero on Turoa rd	2723107	6202308	912
15	Mangawhero @ Turoa rd	2719503	6198649	663
16	Mangaeteroa Stream @ Horopito	2714942	6203708	736
17	Makotuku River @ Horopito	2715050	6203696	713
18	Orautoha stream @ Middle rd	2713091	6205484	712
19	Taurewa stream d/s intake	2730850	6235993	621
20*	Tauwhitikuri Stream d/s intake	2730873	6236020	621
21*	Mangatepopo d/s dam	2730962	6236051	624
22	Tauwhitikuri Stream u/s intake	2731045	6233786	728
23	Okupata d/s intake	2728772	6235536	694
24*	Whakapapa d/s intake	2723280	6228877	680
25	Whakapapa u/s intake	2723465	6228824	697
26*	Whakapapanui @ SH4	2726914	6225525	835
27*	Whakapapaiti @ SH4	2723631	6222537	859
28*	Trib of Ohinepango @ old hut	2740786	6218482	1106
29*	Ohinepango Springs	2741269	6217420	1091
30*	Waihohonu Springs	2740293	6220717	1158
32*	Wahianoa stream u/s intake	2737514	6199145	934
33*	Unnamed Karioi forest stream	2736402	6199318	935
34*	Te Ununuakapuataariki stream	2730309	6192788	701
35	Waiharakeke stream	2733203	6192405	735
36	Unnamed Karioi forest stream	2732704	6193961	725
37	Unnamed Karioi forest stream	2733009	6194725	749
38	Unnamed Karioi forest stream	2740109	6198462	914
39	Mangatawai @ Tongariro confluence	2750705	6221184	660
40*	Tongariro d/s Poutu intake	2754050	6226836	456
41	Waitaki stream d/s Rotokura lake	2726571	6192156	627
42	Waiharuru trib	2725422	6196222	710
43	Waiharuru stream	2725000	6196222	710

Site no.	Site name	Easting	Northing	Altitude
44*	Makomiko stream	2716563	6216130	746
45	Unmarked spring	2725250	6198400	770
46*	Mangaturuturu river	2716300	6208300	820
47*	Waipakihi @ end of road	2749450	6216500	857
48*	Tongariro d/s Rangipo dam	2750083	6218070	813
49*	Tongariro @ pillars of hercules	2750900	6220800	660

Appendix 3: Raw invertebrate data from 16 study sites (Chapter 3) in Tongariro National Park and Hawke's Bay of the North Island of New Zealand collected on four occasions between February 2008 and July 2009. Values are mean number of individuals collected from five Surber samples (area = 0.1 m²) at each site on each occasion. Site names are give in Table 1 in Chapter 3. 0208 = February 2008, 1008 = October 2008, 0209 = February 2009, 0709 = July 2009.

No.	Taxon	NP1.0208	NP2.0208	NP3.0208	NP4.0208	NP5.0208	NP6.0208	NP7.0208	NP8.0208
Ephemeroptera									
1	<i>Deleatidium</i> spp.	0	11.2	70.4	94.8	3.6	5	19.6	96.8
2	<i>Nesameletus ornatus</i>	0	0	1.4	0	0	0	0	0
3	<i>Coloburiscus humeralis</i>	0	0	26.4	0.6	0	0	0	100.4
4	<i>Acanthophlebia cruenata</i>	0	0	0.2	0	0	0	0	0
5	<i>Austroclima sepia</i>	0	0	29.2	0	4.2	0	0	8.2
6	<i>Austroclima jollyae</i>	0	0	0	3	0	2	4	7.6
7	<i>Mauiulus luma</i>	0	0	0	0	0	0	0	0
8	<i>Zephlebia spectabilis</i>	0	0	2	0	0	0	0	0
9	<i>Zephlebia versicolor</i>	0	0	0.2	0	0	0	0	0
10	<i>Zephlebia dentata</i>	0	0	0	0	0	0	0	0.2
11	<i>Zephlebia tuberculata</i>	0	0	0	0	0.2	0	0	0
12	<i>Amelotopsis perscitus</i>	0	0	0	0	0	0	0	0
13	<i>Neozephlebia scita</i>	0	0	4	0	0	0	0	0.4
Plecoptera									
14	<i>Zealandoperla</i> spp.	0	31.4	8.8	25.8	2.6	4.4	14.2	71.8
15	<i>Zealandobius confusus</i> gp.	0	0.6	0	0.4	2.2	0	0	1.2
16	<i>Austroperla cyrene</i>	0	0.6	1.6	1	0	0	0.2	7
17	<i>Stenoperla prasina</i>	0	0	0.4	0	0	0	0	0
18	<i>Taraperla pseudocyrene</i>	0	0.2	2.8	0	0	0	0	0
19	<i>Megaleptoperla grandis</i>	0	5.8	0.2	3.6	0	1.6	0.6	6.6
20	<i>Megaleptoperla diminuta</i>	0	0	0	0	0	0	1.8	0
Trichoptera									
21	<i>Aoteapsyche colonica</i>	0	22	3.2	7.8	0	13.6	11.6	172.8
22	<i>Orthopsyche fimbriata</i>	0.2	0	0	0	0	0	0	1
23	<i>Orthopsyche thomasi</i>	0	0	0.2	0	0	0	0	0
24	Early instar Hydrobiosidae	0	3.4	8	4.6	5.6	4	1.8	0
25	<i>Psilochorema</i> A	0	0	2.2	1.2	0	0	0	0
26	<i>Psilochorema</i> B	0	0	0	0	0	0	0	1.2
27	<i>Psilochorema</i> C	0	0	0	0	0	0	0	0.4
28	<i>Psilochorema</i> D	0	0	0	0	0	0	0	0
29	<i>Psilochorema</i> E	0	0	0	0	0	0	0	0
30	<i>Hydrobiosis parumbripennis</i>	0.4	1	4	1.8	2.4	2	3.4	2
31	<i>Hydrobiosis umbripennis</i>	0	0	0	0	0	0	0	0

No.	HB1.0208	HB2.0208	HB3.0208	HB4.0208	HB5.0208	HB6.0208	HB7.0208	HB8.0208	NP1.1008	NP2.1008	NP3.1008	NP4.1008
1	76.4	368	49.6	22.4	109.6	128	1.2	8	1.6	10	38	66
2	0	0	0	0	0	0	0	0	0	0	0.4	3.2
3	0.6	0	0.4	0	1.2	0.4	0	0	0	1.2	60.4	2.8
4	0	0	0	0	0	0	0	0	0	0	0	0
5	0.8	0	13.6	11.2	4.4	10.4	0	17.2	3.44	0	31.6	0.8
6	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	1.6	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	7.2	4.8	0	1.6	0	1.8	0.36	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	4.8	0
14	0	0	0	0	0	0	0	0	0	3	16	1.8
15	0	0	0	0	0	0	0	0	0.2	0.2	0	0
16	0	0	0	0	0	0	0	0	0	0.6	0.8	1.6
17	0	0	0	0	0	0	0	0	0	0	0.8	0.8
18	0	0	0	0	0	0	0	0	0	0	0.4	0
19	0	0	0	0	0	0	0	0	0	2.6	0	3.2
20	0	0	0	0	0	0	0	0	0	0	0	0
21	8.8	8.8	112.8	32.8	199.2	483.2	6.8	9	1.8	1.6	0.2	2
22	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0.2	0.6	0	0
24	0	0	0	0	1.8	0	4.4	0.8	0.96	0	5.2	0.8
25	9.2	6.4	3.4	2.4	4.4	8	0	0	0	0	0	0
26	0	0	0	0	0	0	0	5.4	1.08	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0.8
29	0	0	0	0	0	0	0	0	0	0	0	0
30	3.2	7.2	1.6	8	4.2	4	5.8	0.8	0.16	0	0	0
31	0	0	0	0	0	0	0	1	0.2	0	0	0

No.	NP5.1008	NP6.1008	NP7.1008	NP8.1008	HB1.1008	HB2.1008	HB3.1008	HB4.1008	HB5.1008	HB6.1008	HB7.1008	HB8.1008
1	1.4	1	53	12.4	87.6	165.2	145.2	9.4	86.8	84.8	8	30.8
2	0	0	1	0	0	0	0	0	0	0	0	0
3	0	0	0.4	6.8	0	0	2.4	0	0.8	0.2	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	1.6	0	0	26.6	2	0	0.8	21.6	6
6	0	0	0.2	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	3.2	0	0	0	0.8	2.8
12	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	3.6	0	0	0	0	0
14	0.2	2.4	0.2	3.2	0	0.4	0	0	0	0	0	0
15	0	0	0.2	0.2	2.8	1.2	0.8	0	7.6	0.4	0	0
16	0	0	0	0.2	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0.2	0.2	0	0	0	0	0	0	0	0	0
20	0	0	4.8	0	0	0	0	0	0	0	0	0
21	0.2	1.6	1	1	0.4	0	20	1.8	2	1.6	9.8	1.6
22	0	0	0.4	1.2	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	3.4	0	0	0	0	0.6	0	2.4	1.8	0
25	0	0	0	0	2	0.8	0	0.2	1.2	1.2	1.4	0
26	0	0	0	0	0	0	0	0	7.2	0	0	0
27	0	0	0.2	0	0	0	0	0	0	0	0	0
28	0	0	0.8	0	0	0	0	0	0.8	0	0	0
29	0	0	0	0	0	0	0	0	0	0	6.4	3.2
30	0.2	0.2	0	0.2	0	0.4	0.4	0.2	0	2.2	4	0
31	0	0	0	0	0	0	0	0	0	0	0	0

No.	NP1.0209	NP2.0209	NP3.0209	NP4.0209	NP5.0209	NP6.0209	NP7.0209	NP8.0209	HB1.0209	HB2.0209	HB3.0209	HB4.0209
1	0.2	6.2	29.8	31.8	5.6	0.2	54.2	43.8	192.4	62	173.6	46
2	0	0	0.2	0	0	0	0	1.8	0.4	0.2	0	0
3	0.2	0.6	25.6	0.4	0	0	0.8	63.8	0.8	0	2.6	0
4	0	0	0	0	0	0	0	0	0	0	0	0
5	0	1	49.6	0.2	0.2	0	0.2	3.8	0	0	55.2	8.6
6	0	0	0	0	0	0	0	0.8	0	0	0	0
7	0	0	2.4	0	0	0	0	0	0	0	0	0
8	0	0	3	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	4.8	3
11	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0.2	0	0	0	0	0	0	0	0	0
13	0	0	5.6	0	0	0	0	0	0	0	4	0
14	0.2	24.4	6	16.4	3.2	0.4	12.8	26.4	1.4	0	0	0
15	0	0.2	0.8	0.2	1	0.2	0	0.8	0	0	0	0
16	0	2.4	2.2	0	0	0	0.2	6.4	0	0	0	0
17	0	0	0.2	0	0	0	0	0	0	0	0	0
18	0	0	0.2	0	0	0	0	0	0	0	0	0
19	0	1	0	0	0	0	1.2	7.4	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0
21	0	14.6	0.8	0.2	0	0.6	3	67.8	5	6.4	363.2	14.4
22	0.4	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0
24	0.4	0	12	0.8	0	0.2	3.4	6	0.4	2.6	0.8	0.8
25	0	0	3.6	1	0	0	0.8	0	3	2	3	0
26	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0.6	0	0	11.2	0	1.8	5.6	2.6	1.2	4	3
31	0	0	0	0	0	0	0	0	0	0	0	0

No.	HB5.0209	HB6.0209	HB7.0209	HB8.0209	NP1.0709	NP2.0709	NP3.0709	NP4.0709	NP5.0709	NP6.0709	NP7.0709	NP8.0709
1	134.8	276.4	0	8.6	0.4	9.2	11.4	44.4	4	1.8	108.2	81.2
2	0.2	0	0	0.2	0	0.4	0.2	0.8	0	0	0.8	2.8
3	1.8	0	0	0	0	0.8	8	0.2	0	0	8.8	44.2
4	0	0	0	0	0	0	0	0	0	0	0	0
5	3.8	12.4	0	12.8	0	0	12	0.2	6.4	0	0	5.4
6	0	0	0	0	0	1	0	0	0	0	1	0.2
7	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0.2	0	0.8	0	0	0	0	0	0	0	0.2
11	0	0	0	6.2	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	1.4	0	0	0	0	1
14	0.2	0	0	0	0.2	24	2	2.8	0.6	5	3	11
15	0	0	0	0	0	0.4	0.4	0.2	29.2	0	3.4	3.8
16	0	0	0	0	0	0.6	0.2	0	0	0	6	2
17	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0.2	0	0	0	0	2.8	1.2
20	0	0	0	0	0	0	0	0	0	0	0	0
21	50.2	113.8	0	1.6	0.2	2.4	0	0	0	0	3.4	19.2
22	0	0	0	0	0	0.2	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0.6
24	1	0.8	2.4	0.6	1.6	1	2.2	2	4.6	2.2	11.8	5.4
25	0	6	0	6.2	0	0.2	0.2	0.2	0.4	0	5.8	0.6
26	1.8	1.2	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0.8	2.4	0	0	0	0	0	0	0	0
30	3	12.6	22.4	0	0	0.8	0	2.6	0.4	0.2	2.8	3.4
31	0	0	0	6	0	0	0	0	0	0	0	0

No.	HB1.0709	HB2.0709	HB3.0709	HB4.0709	HB5.0709	HB6.0709	HB7.0709
1	18.8	52.6	110.2	37.4	79.6	45.2	4.4
2	0	0	0	0	0.2	0	0
3	0	0	1.4	0	1.6	0	0
4	0	0	0	0	0	0	0
5	0	0	37.8	3.8	0	0	5
6	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0
10	0	0	3.6	1.2	0.8	0.2	0
11	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0
13	0	0	4	0	0	0	0
14	0.2	0.4	0	0	0	0	0
15	1	2	0	0	9.4	0.2	0
16	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0
21	0	1	177.6	1.2	2	2.4	1
22	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0
24	0.2	0.4	2.2	1	0.4	0	0
25	0	0.2	0.2	1.6	1	0.8	4.6
26	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0
30	0	0.2	2	1.4	0.2	1.2	2.2
31	0	0	0	0	0	0	0

No.	Taxon	NP1.0208	NP2.0208	NP3.0208	NP4.0208	NP5.0208	NP6.0208	NP7.0208	NP8.0208	
32	<i>Hydrobiosis frater</i>	1	0	0	0	0	0	0	0	
33	<i>Hydrobiosis spatulata</i>	0	0	1.8	0	0	0	0	0	
34	<i>Hydrobiosis clavigera</i>	0	0	1	0	0	0	0	0	
35	<i>Hydrobiosis harpidosa</i>	0	0	0	0	0	0.4	0	0	
36	<i>Hydrobiosis charadrea</i>	0	0	0	0	0	0	0	0	
37	<i>Neurochorema forsteri</i>	0	0	0	0	0	0	5	1	
38	<i>Neurochorema confusum</i>	0	0	0.2	0	0	0	0	0	
39	<i>Costachorema callistum</i>	0.6	0.4	0.6	1.6	0	0.4	2.8	0.6	
40	<i>Costachorema xanthopterum</i>	0	0.4	0	0	0	0	0	0	
41	<i>Hydrobiosella mixta</i>	0	0	0	0	0	0	0	0	
42	<i>Hydrochorema crassicaudatum</i>	0	0	0	0	0.2	0	0	0	
43	Caddis Pupae	0	0	0	0	0	0	0.8	0	
44	<i>Plectrocnemia machlachlani</i>	0	0	0	0	0	0	0	0	
45	<i>Polyplectropus</i> sp.	0	0	0	0	0	0	0	0	
46	<i>Pycnocentria evecta</i>	0	0	4	0	0	0	0.2	1.4	
47	<i>Pycnocentria funerea</i>	0	0	1	0	0	0	0	1.4	
48	<i>Pycnocentria hawdonia</i>	0	0	0	0	0	0	0.8	0	
49	<i>Pycnocentria sylvestris</i>	0	0	0	0	0	0	0	0	
50	<i>Pycnocentria gunni</i>	0	0	0	0	18.6	0	0.4	0	
51	<i>Pycnocentroides aeris</i>	0	0	0.6	0	1.2	0	1.2	17.4	
52	<i>Beraeoptera roria</i>	0	0.6	6.6	5.4	0	0.2	1.6	225.2	
53	<i>Confluens hamiltoni</i>	0	0	15.6	1.6	0	0	2.4	1.6	
54	<i>Oeconesus similis</i>	0	0	0	0	0	0	0	0	
55	<i>Hudsonema amabile</i>	0	0	0.2	0	0	0	0	0	
56	<i>Hudsonema alienum</i>	0	0	0	0	0	0	0	0	
57	<i>Triplectides dolichos</i>	0	0	0	0	0	0	0	0.2	
58	<i>Triplectides obsoletus</i>	0	0	0	0	0	0	0	0	
59	<i>Oxyethira albiceps</i>	0.2	0.4	6.8	1.6	0	0	0	0.6	
60	<i>Paroxyethira</i> sp.	0	0	0	0	0	0	0	0	
61	<i>Olinga feredayi</i>	0	0	1.8	0.4	0	0	0	4.8	
62	<i>Helicopsyche poutini</i>	0	0	0.6	0	0	0	0	0.6	
63	<i>Pseudoeconesus</i> sp.	0	0	0	0	0	0	0	0	
64	<i>Zelolessica cheira</i>	0	0.4	14.6	1.2	1	0.6	2	0.8	
65	<i>Allocentrella</i> sp.	0	0	3.4	0	0	0	0	0	
Diptera										
66	Orthocladiinae A	0.6	0	0.2	0	0	0	0	0.8	
67	Orthocladiinae B	0	19.8	0	55.2	12.8	39.2	53.4	8	
68	Orthocladiinae C	0	0	4.2	93.4	13.6	4.8	0	0.2	
69	Orthocladiinae D	0.2	6.6	0	9.2	0	5	0	0	
70	Orthocladiinae E	0	12.2	67	35.8	63.6	2.2	6.4	0.8	
71	Orthocladiinae F	0	0	0	0	0	0	0	0	
72	Orthocladiinae Z	0	0	0	0	0	0	0	0	

No.	HB1.0208	HB2.0208	HB3.0208	HB4.0208	HB5.0208	HB6.0208	HB7.0208	HB8.0208	NP1.1008	NP2.1008	NP3.1008	NP4.1008
32	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0.8	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	3.2	0	0	0	0	0	0	0	1.2	0
38	0	0	0	0.4	0	0	0	0	0	0	0	0
39	0.8	0	2.4	0	0	0	0	0	0.4	0.6	0	2.4
40	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0
46	0.8	4	306.4	6	2.4	12	0.2	63.2	12.64	0	25.6	0
47	0	0	0	0	2.4	0	0	0	0	0.8	2.4	0
48	0	0	0	0	0	0	1	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0
51	4.8	6.4	367.2	13.6	88	255.2	20	52.8	10.56	0	0	4
52	0	0	0	0	0	0	0	0	0	12	7.6	72.4
53	0	0	0	0	0	0	0	0	0	0	4.8	0
54	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0.8	0	0	0.2	2.4	0.48	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	3.2	0
58	0	0	0	0	0	0	0	0	0	0	0	0
59	0	0	0.8	17.6	0	0.2	37.8	60.8	12.36	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0
61	10	11.2	19.2	0.8	8.2	20	0.2	0	0	0	5.6	0
62	0	0	5.6	0	0	0	0	0	0	0.2	0	0
63	0	0	0	0	0	0	0	0	0	0	0	0
64	0	0	0	0	0	0	0	0	0	0.4	26.8	0
65	0	0	0	0	0	0	0	0	0	0	6.4	0
66	0	0	0	0	0.8	0	0	0	0	0	2.4	1.6
67	0	0	0	0	0	0	0	0	0.4	0.2	21.2	34
68	0	2.4	22.4	5.6	2.4	13.6	5.2	0.8	0.16	4.2	0	10.4
69	0	0	0	0	0	0	0	0	0.4	0.8	2.8	110.4
70	22.8	13.6	12.8	152.4	12.8	10.4	19.2	7.2	1.44	0.6	33.2	24.8
71	0	0	0	11.2	0	0	0	2.4	0.48	0	0	0
72	0.8	0	7.2	0	0	0	0.8	0	0	0	0	0

No.	NP5.1008	NP6.1008	NP7.1008	NP8.1008	HB1.1008	HB2.1008	HB3.1008	HB4.1008	HB5.1008	HB6.1008	HB7.1008	HB8.1008
32	0	0.4	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0.2	0	0	0	0.2	0	0	0	0	0
38	0	0	0	0	0	0	0.2	0.2	0	0	0	0
39	0	1	0	0.2	0.6	0	2.6	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0.2	0.2	0.2	0	0	0	0	0
45	0	0	0	0.2	0	0	0	0	0	0.2	0	0.4
46	0	0	0	0	0	0	19	0.2	0.2	0.4	27.2	8.2
47	0.2	0	0	1.2	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0
51	0	0	0.8	0.2	18.6	6.4	120.8	3	28.2	106	432	36.2
52	0	0	24.8	23	0.8	0.8	0	0	0	0	0	0
53	0	0	0.2	0.2	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0.2	0	0	0	0.4	11	0
56	0	0	0	0	0	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0	0	0
59	0.2	0	0	0	0.2	0.2	0	2	0	0	0	0.2
60	0	0	0	0	0	0	0	0	0	0	0	0
61	0	0	0.4	0	1.2	0.6	9.8	0	0.4	0.6	0	0
62	0	0	0	0	0	0	19	0	0	0	0	0
63	0	0	0	0	0	0	0	0	0	0	0	0
64	0	0	0.2	0	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0
66	0	8.2	2.2	0	0	0	0	0	0	0	0	0
67	19.6	18.2	18.8	118.6	0	1.2	71.2	163	0	92	9.8	5.4
68	0	2.4	0	0	0	0	0	0	0	0	0	0
69	0.8	0.4	39.2	12.6	1.2	0.8	16.4	233.8	0	61.4	3.2	1.6
70	0.2	4.8	6.2	19	0.4	0.6	3.2	181.6	0	0.6	8	5.2
71	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0.2	0	0.6	0	0	0	0

No.	NP1.0209	NP2.0209	NP3.0209	NP4.0209	NP5.0209	NP6.0209	NP7.0209	NP8.0209	HB1.0209	HB2.0209	HB3.0209	HB4.0209
32	0	0	0	0.2	0	0	0	0	0.4	0	0	0
33	0	0	2	0	0	0	0	0.2	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	2.4	0.2
35	0	0	0	0	0	0	0	0	0	0	0	0
36	0.4	0	0	0	0	0	0	0	0	0	0	0
37	0	0.8	0	0	0	0	0.8	0.2	0	0	24	0
38	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0.8	0	0	0	1	5.4	0	0	4	0
40	0	0	0	0	0	0	0	0	0	0.2	2.4	0
41	0	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0.2	0	0	0
46	0	0	0	0	0	0	0	0	3.4	0.4	300	15.4
47	0	0	0	0	0	0	0.4	4.8	0	0	0	0
48	0	0	0.6	0	0	0	0	0	0	0	0	0
49	0	0	5.8	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0
51	0.2	0	2.8	1.4	0.8	0	1	0.2	43	11.2	380.8	34.4
52	0	2.8	1.6	1.8	0	0.2	1.4	50	1.6	0	0	0
53	0	0	13	0	0	0	0	0	0	0	0	0
54	0	0.2	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0.2	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0	0	0
59	0	1.6	0	0	0.2	0	0	0.8	0.8	0	0	1.6
60	0	0	0	0	0	0	0	0	0	0	0	0.8
61	0	1	0.2	0	0	0	0	4.4	12.4	4	66.4	0
62	0	0.2	0	0	0	0	0	0	0	0	20.8	0
63	0	0	0	0	0	0	0	0	0	0	0	0
64	0	1.2	12	0.6	0	0	0	1	0	0	0	0
65	0	0	4.2	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0.8	0	0	0	0	0
67	4	40.8	12	2	115	2.4	55.8	25.8	17	35.6	47.2	148.4
68	0	4.6	0	0	0	0	0	0	0	0	0	0
69	0	2.4	1.8	0	45.8	0.2	2	0.2	0	5	4	9.4
70	0.4	2.4	3	0	32.6	1.2	0.6	2.8	0	1.8	0	9.2
71	0	0	0	0	0	0	0	6	0	0	0	12.2
72	0	0	0	0	0	0	0	0	0	0	0.8	0

No.	HB5.0209	HB6.0209	HB7.0209	HB8.0209	NP1.0709	NP2.0709	NP3.0709	NP4.0709	NP5.0709	NP6.0709	NP7.0709	NP8.0709
32	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0.2	0.8	0	8.2	0	0	0.4
34	0.2	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	1	0	0	0	0	0	0	0
37	0	0	0	0	0	0.4	0	0	0	0	3.8	2
38	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0.2	0	0.4	1.6	0.2	1	0.8	2
40	0	0	0	0	0	0	0	0	0	0	0	0.4
41	0	0	0	0	0	0	0.2	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0
44	0.2	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	1.2	0	0	0	0	0	0	0	0
46	8.4	2.8	0	12.4	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0.8	0.8	2.2	0	6	5.4
48	0	0	0	0	0	0	4.6	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0
51	95.8	92.4	1.6	14.2	0	0	0.6	0.2	1.2	0	6.4	3.4
52	0	0	0	0	0	10.2	6.4	1.8	0	1	110.6	138.8
53	0	0	0	0	0	0	1.2	0.2	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0
55	0.4	0.2	0.8	0	0	0	0	0	0	0	0	0.2
56	0	0	0	0	0	0	0.4	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0	0.2
58	0	0	0	0.2	0	0	0	0	0	0	0	0
59	0	0	2	4.8	0	0.2	0	0.8	0.2	0	0	0.2
60	0	0	0	0	0	0	0	0	0	0	0	0.2
61	8.2	6.4	0	0	0	0	0.2	0	0	0	0	0.8
62	0	0	0	0	0	0	0	0	0	0	0	0
63	0	0	0	0	0	0	0	0	0	0	0.2	0
64	0	0	0	0	0	0.8	12.6	0.8	0	0	0	0
65	0	0	0	0	0	0	2.4	0	0	0	0	0
66	0	0	0	0	0.2	0	0	0	0	11.2	5.4	0
67	25.8	1.6	199.4	17.2	166.6	18.8	6	186.2	32.8	124.8	19.4	1
68	0	0	0	0	0	28.2	0	0	9	0	0	0
69	5.4	314.4	43.8	19.2	0.8	0	0	8	2.6	0	5.2	0
70	0	0	12.4	9	0	7.8	0	20.2	32.6	0	24	2.4
71	0	0	9.2	0	0	0	0	0	0	0	0	1
72	0	0	0	20.4	0	0	0	0	0	0	0	0

No.	HB1.0709	HB2.0709	HB3.0709	HB4.0709	HB5.0709	HB6.0709	HB7.0709
32	0	0.2	0	0	0	0	0
33	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0
37	0	0	13	0	0	0	0.2
38	0	0	0	0	0	0.2	0
39	0	0	0	0	0	0	0
40	0	0	1.4	0	0	0	0
41	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0
45	0	0	0	0.6	0	0	0
46	0	0	146.6	9	1	1	17.2
47	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0
51	1.4	1.2	338.2	44.4	0.6	5.4	196.6
52	0.2	0	0	0	0	0	0
53	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0
55	0	0	0	1	0.4	0	16.4
56	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0
61	0	0.4	13.8	0	1.6	1.2	1.4
62	0	0	16	0	0	0	0
63	0	0	0	0	0	0	0
64	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0
66	0	0	0	0	0	0.2	0
67	1.6	0.4	44.4	7.2	2.8	1	0.8
68	0	0	0	0	0	0	0
69	0.4	0	7	1.8	0	0.6	0
70	0	0	0	3.4	0	0	0
71	0	0	0.8	0	0	0	0.2
72	0	0	0	0	0	0	0

No.	Taxon	NP1.0208	NP2.0208	NP3.0208	NP4.0208	NP5.0208	NP6.0208	NP7.0208	NP8.0208
73	Chironominae A	0	11.8	2	4.6	16	1.8	9	1.6
74	Chironominae B	0	0	0	0	0	0	0	0.8
75	<i>Maoridiamesa</i> sp.	0	101.6	1	11.6	176.2	17.2	92.6	8.6
76	Tanypodinae	0	0	1.4	0.8	0.8	0	0	0.4
77	Chironomidae pupae	0	4.2	3.4	2.8	1.2	0.4	2.6	0.2
78	Eriopterini (other)	0	5.8	0	1.6	0.4	3.2	4.2	0.6
79	<i>Molophilus</i> sp.	1.2	0	0	0	0	0	0	0
80	<i>Aphrophila neozelandica</i>	0	0.6	3.6	7.2	0.2	0.8	1.2	13.8
81	<i>Austrosimulium</i> spp.	0	15.6	1.8	0	3	1.8	0.2	0
82	<i>Mischoderus</i> sp.	0	0.2	0	0	0	0	0.4	2.4
83	Empididae	0	2.6	0	0	7.4	3.6	0	0
84	Ceratopogonidae	0	0	0	0	0	0	0	0
85	<i>Limonia</i> sp.	0	0	0	0	0.2	0	0	0
86	Ephydriidae	0	0	0	0	0	0	0	0.2
87	Muscidae	0	0	0.2	4.8	2.4	3.4	5.8	0
88	<i>Paralimnophila</i> sp.	0	0	0	0	0	0	0	0
89	Stratiomyidae	0	0	0.4	0	0	0	0	0
90	Unidentified Diptera	0	0	0	0	0	0	0	0
	Coleoptera								
91	Elmidae <i>Hydora</i> spp.	0	6.6	15.2	42	0.4	1.6	35.6	15.4
92	Hydraenidae	0	0	6	0.2	0	0	0	1.6
93	Hydrophylidae	0	0	0.2	0	0	0	0	0
94	Ptilodactylidae	0	0	5	0.2	0	0	0	0
95	Scirtidae	0	0	0	0	0.2	0	0	0
	Mollusca								
96	<i>Potamopyrgus antipodarum</i>	0	0	14.4	0	0	0	0	0.2
97	<i>Physa</i> spp.	0	0	0	0	0	0	0	0.2
98	<i>Ferissia</i> spp.	0	0	0	0	0	0	0	0
99	<i>Latia neritoides</i>	0	0	0	0	0	0	0	0
100	<i>Gyraulus corinna</i>	0	0	0	0	0	0	0	0
101	<i>Sphaerium novaezelandiae</i>	0	0	0	0	0	0	0	0
	Other								
102	<i>Archichaulioides diversus</i>	0	0	15.6	0.4	0	0	0.2	64.2
103	Platyhelminthes	0	1.4	0.8	0	0.2	0.2	0	2.8
104	Oligochaeta	0	0.2	2	4.8	59.4	55.4	0.4	1.4
105	Nematomorpha	0	0	0	0	0.2	0	0	0
106	<i>Paricalliope</i> spp.	0.2	0	0	0	0	0	0	0
107	Ostracoda	0	0	0	0	0	0	0	0
108	Hirudinea	0	0	0	0	0	0	0	0
109	Nemertea	0	0	0	0	0	0	0	0
110	Nematoda	0	0	0	0	0	0	0	0
111	<i>Xanthocnemia zelandica</i>	0	0	0	0	0	0	0	0

No.	HB1.0208	HB2.0208	HB3.0208	HB4.0208	HB5.0208	HB6.0208	HB7.0208	HB8.0208	NP1.1008	NP2.1008	NP3.1008	NP4.1008
73	1.6	1.6	15.2	176.6	7.2	61.6	27.8	24	4.8	5.2	4.8	8
74	0	0	0	0	0	0	0	0.2	0.04	0	0	0
75	0	0	0.2	0	0	0	3.2	0	0	0.8	0	47.2
76	0	0	0	0	0.8	0	0	0	0	0	0.8	0
77	0	0	4	32.8	0	5.6	1.8	1.6	0.32	0	2.4	3.2
78	0.4	2.4	0	0.8	6.6	12	0	0	0	0.8	0	5.2
79	0	0.2	0	0	0.4	0	0	0	0	0	0	0
80	0	0	0	0	1.4	3	0	0	0	0.4	9.2	4.6
81	17.6	8	0	0	2.4	0	2.6	1	0.2	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	2	0
84	0	0	0	0	0	0	0	0	0	0	0.4	0
85	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	2.4	0.2
88	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0
91	37.8	20.8	1.6	25.6	55.2	32.8	0.2	0	0	1.2	25.2	46
92	0	0	0	0	0	0	0	0	0	0	4	0
93	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	6.4	0
95	0	0	0	0	0	0	0	0	0	0	0	0
96	0.8	0	7.2	43.2	8.8	5.4	1175	40.8	8.16	0	4	0
97	0	0	0	3.2	0	0.2	70.8	2	0.4	0	0	0
98	0	0	0	64	0	0	0	7.2	1.44	0	0	0
99	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0.2	0	0	2.4	0	0	0	0	0
101	0	0	0	0	0	0	0	0	0	0	0	0
102	0.2	0.8	1.6	1.6	3.4	1.6	0	0	0	0	21.6	0
103	0	0	19.2	16	0.8	8	25.4	4.2	0.84	0	0	0
104	1.6	5.6	12	44.8	9.6	7.2	692	16.8	3.36	0	0.8	0
105	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	2.6	66.4	0	0.8	15.2	53.6	10.72	0	0	0
107	0.4	0.8	0.8	0.8	0	1	2.6	0	0	0	0	0
108	0	0	0	0.8	0	0	0.4	0	0	0	0	0
109	0	0	0	0	0	0	0	2.4	0.48	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0

No.	NP5.1008	NP6.1008	NP7.1008	NP8.1008	HB1.1008	HB2.1008	HB3.1008	HB4.1008	HB5.1008	HB6.1008	HB7.1008	HB8.1008
73	2	3.2	19.8	6.8	0.4	0.4	2.4	1.2	0.4	7.4	0	0
74	0	0	0	0	0	0.4	0	5.6	0	1.4	0	0
75	15.4	5	14.4	20	0	0	9.6	1	0	0	0	0.2
76	0	0	0	0	0	0.4	0	4.6	0.2	3	0	0
77	1.8	1.8	10	15	0.2	0.2	2.6	70.2	0.6	10.8	0.8	0
78	0.8	2.6	3.2	1	1	1	0	0	2	3.4	0	0
79	0	0.8	0	0	0	0	0	0	0	0	0	0
80	0	3.4	5.8	2.2	0.6	1.8	0	0	3.4	7.2	0	0
81	0.2	0	0	0	1.2	3	0	0	0.6	5.6	4	0.2
82	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0
87	0.8	0.6	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0.2	0
91	0	0.4	15.8	3	3	2.6	0	0.4	2.4	7.6	0	0
92	0	0	0	0	0	0.2	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	7.4	16	0.2	0	135.8	2
97	0	0	0	0	0	0	0	0.2	0	0	4	0
98	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0	0	0	0	0
101	0	0	0	0	0	0	0.8	0	0	0	0	0
102	0	0	0	0	0	0.2	1.8	0	0	0.2	0	0
103	0	0.2	0	0	0	0	36.2	0.4	0	0	1.6	0
104	0.8	0	0	0.4	0	0.2	5.6	108.8	0	32.6	83.4	17
105	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	6.4	81.6	0	0	63.4	552.6
107	0	0	0	0	0	0	0	0	0	0	0	0.2
108	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0
110	0	0.2	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0.2	0	0	0	0

No.	NP1.0209	NP2.0209	NP3.0209	NP4.0209	NP5.0209	NP6.0209	NP7.0209	NP8.0209	HB1.0209	HB2.0209	HB3.0209	HB4.0209
73	0.2	2.8	0.8	0	12.2	0.4	2	3.8	1.4	5.8	4.8	43
74	0	0	0	0	0	0	0	0	0	0	0	0
75	0.4	66.8	0.2	0.4	328.6	2	11.8	1.2	0	0	8	1.2
76	0	0	0.4	0	0	0	0	0	0	0	0	0
77	0	0.6	0	0	12.2	0	3.2	1.8	0.4	0.4	2.4	13.8
78	0	5.4	0	1	0.2	0	6.6	1.2	2.8	2.2	0	1
79	0	0	0	0	0	0	0	0	0	1.2	0	0
80	0	0	4	0.6	0	0	5.8	13	0.2	0.2	0	0
81	0	14.2	0.4	0	2.8	0	0.2	1.8	11.2	1	0	0
82	0	0.2	0	0	0	0	0	0.2	0	0	0	0
83	0	0	0	0	2	0.2	1.4	0	0	0.4	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0.6	0	0	5	0	0.4	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0
91	0	9.2	10.8	18	0	0	20.4	2.4	6.4	11.4	0	13.4
92	0	0	4.6	0	0	0	0	2.8	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0.4	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	2.8	0	0	0	0.8	0	0	0.6	34.4	171.4
97	0	0	0	0	0	0	0	0	0	0	0	6.4
98	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0	0	0	0	0	32.8
100	0	0	0	0	0	0	0	0	0	0	0	0
101	0	0	0	0	0	0	0	0	0	0	0	0
102	0	0.2	9.2	0.2	0	0	1.2	5.2	3	0.4	0.4	3.2
103	0	1.2	0	0	0.8	0	0	0.8	0	0	12	10.6
104	0	0.2	4.6	0.6	23.4	0.2	4.8	1.8	4.6	4.8	12.8	6.8
105	0	0	0	0	0	0	0	0	0	0	0	0
106	0.6	0	0	0	0	0.2	0	0	0.2	0.4	5.6	5.6
107	0	0	0	0	0	0	0	0	0	0	0	0
108	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0.8
110	0	0	0	0	2.4	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0

No.	HB5.0209	HB6.0209	HB7.0209	HB8.0209	NP1.0709	NP2.0709	NP3.0709	NP4.0709	NP5.0709	NP6.0709	NP7.0709	NP8.0709
73	3	444.8	106.2	18	0	0	0	0	6.6	0	3.2	0.4
74	0	0	0	9.2	0	0	0	0	0	0	0	0
75	0.8	0	0.8	0	24.8	26	1	88.6	168.6	16.8	63.4	19.2
76	0	0	0	1.6	0	0	0	0	0	0	0	0
77	1	32.4	16.8	1.4	2.6	0	0	2.4	0.8	3	0.2	0.4
78	2.2	5.8	0	0	0	1.4	0	2.2	0.6	2.8	4.8	2.8
79	0	0	0	0	1	0	0	0	0	0	0	0
80	1.2	2	0	0	0	0.4	1	0.8	0	0	5	5.4
81	1.6	1	1.2	1.6	0.2	12.4	0	0	1	7	0.8	0
82	0	0	0	0	0.2	0	0	0	0	0	0.2	0
83	0	0	0	0	0	0	0.2	0	0	0	0.8	0
84	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0.2	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0.6	0	0	0	0.8	0	0.4	4.2	0	0	0.2
88	0	0	0	0	0	0	0	0	0	0	0	0.2
89	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0
91	42	47.8	0	0	0	0.6	4.8	1.6	0	1	19.4	1
92	0	0	0	0	0	0	0.6	0	0	0	0	1
93	0	0.2	0	0	0	0	0.6	0	0	0	0	0
94	0	0	0	0	0	0	0.4	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0
96	11.6	17.4	453	52.8	0	0	0	0	0	0	0	0
97	0	0	10.8	0	0	0	0	0	0.2	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0	0	14.4	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0	0	0	0	0
101	0	0	0	1	0	0	0	0	0	0	0	0
102	1.8	3.8	0	0	0	0.2	0.4	0	0	0	0	1
103	1	16.8	2.4	5.6	0	0	0	0	0	0	0.2	0.2
104	12	3.4	524.6	132.6	0.2	0.2	0.4	2.6	0.8	0	12	0.2
105	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	4.8	121.2	0	0	0	0	0	0	0	0
107	0	6.6	0	0.4	0	0	0	0	0	0	0	0
108	0	0	0.2	0	0	0	0	0	0	0	0	0
109	0	2	0	2	0	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0

No.	HB1.0709	HB2.0709	HB3.0709	HB4.0709	HB5.0709	HB6.0709	HB7.0709
73	0	0	8	0.2	0	0	0.2
74	0	0	0	0	0	0	0
75	2.2	0.2	12.2	0.6	0	0	0
76	0	0	0	1.8	0	0	0
77	0	0	0.8	0.4	0	0	0
78	0.2	0	0	0.2	1	1	0
79	0.2	0.2	0	0	0.2	0	0
80	0	0.2	0	0	0	0.2	0
81	0	0.4	0	0.4	0.2	0.8	0.2
82	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0.2
89	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0
91	0	0	0.2	0.4	0.4	0	0
92	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0
96	0	0	2	39.2	0	0.2	102
97	0	0	0	1.8	0	0	4
98	0	0	0	0	0	0	0
99	0	0	0	0.2	0	0	0
100	0	0	0	0	0	0	0
101	0	0	0	0	0	0	0
102	0.2	0.4	0	0	0.4	0	0
103	0	0	27	7	0	0	1
104	0	0.6	4.6	4.4	0	0	33.8
105	0	0	0	0	0	0	0
106	0	0.6	9	54.2	0	0	60.2
107	0	0	0.2	0	0	0	0
108	0	0	0	0	0	0	0.4
109	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0

Appendix 4: Raw invertebrate data collected from 24 streams of Cantabria, Spain, July 2007 (Chapter 4). Values are mean number of individuals collected from five Surber samples (area = 0.1 m²) at each site. E = Ephemeroptera, P = Plecoptera, TC = cased caddisfly, TF = free-living caddisfly, TN = net-spinning caddisfly, D = Diptera, DC = Chironomidae, CA = adult Coleoptera, CL = larval Coleoptera, O = Other. The taxa contributing the most to group differences are as follows: D1 = *Prosimulium* spp., E1 = *Baetis* spp., O1 = *Echinogammarus* spp., DC4 = Orthoclaadiinae b, E3 = *Ephemerella* sp., O3 = *Bythinella* sp., P1 = *Protonemura* sp., TN1 = *Hydropsyche* sp., DC1 = Orthoclaadiinae a, O2 = Oligochaeta. Site names are given in Appendix 1 of Chapter 4.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12
Ephemeroptera												
E1	280.4	335.2	150.8	73	189.8	1492	73.6	65.8	128	81.8	158.4	238.2
E2	3.2	1.8	4.8	0.2	19	8	2.4	13.4	12.8	9.6	1	3.8
E3	18	49.2	80.4	39.2	36	19.2	2.2	0	4.8	1	1	6.2
E4	0	0	0	0	0	0	0	0	0	0	0	0
E5	0	0	0	0	0	0	0	0	0	0	0	0
E6	0	0	0	0	1.6	0	1.2	0.4	0.4	0.4	0	0.4
E7	0	0	0	0	0	0	0.4	0	0	0	0	0
E8	0	0	0	0	0	0	0	0	0	0	0	0.8
Plecoptera												
P1	4.4	8.6	4.8	4.8	1.6	0	6.4	1	28.4	18.8	4	3
P2	0	0	0	0	1	0	0	0	0.4	0	0	0
P3	0	0	0	0.8	0	0	0	0	0	0	0	0
Trichoptera												
TC1	0	0	0	1.6	0	0	0	0	0	0.2	0.8	0
TC2	0	0	0	0	0	0	0	0	0	0	0	0
TC3	0	0	0	0	0	0	0	0	0	0	0	0
TC4	3.2	0	0.8	0	0.8	0	0	0	0	0	0	0
TC5	0	0	0	0	0	0	0	0	0	0	0	0
TC6	0	0	0	0.2	0	0	0	0	0	0	0	0
TC7	0	0	0	0	0	0	0	0	0	0	0	0
TC8	0	0	0	0	0	0	0	0	0	0	0	0
TC9	0	0.2	0	0	0	0	0	0	0	0	0	0
TC10	0	0.4	0	0	0	0	0	0	0	0	0	0
TF1	12	13.2	6.8	10.2	2.6	3.8	1.4	2	3.6	4.4	4.6	1.2
TF2	0	0	0	0	0	0	0	0	0.8	0	0	0
TF3	0	0.8	0	0	0	0.2	0.8	0	1.8	0	0	0.2
TF4	0.8	0	0	0	0	0	0.8	0	0.8	0	0	0
TF5	0	0	0	0	0	0	0	0	0	0	0	0
TF6	0	0	0	0	0	0	0	0	0	0	0	1
TF7	0	0	0	0	0	0	0	0.2	0	0	0	0.8
TF8	0	0	0	0	0	0	0	0	0	0	0	0
TN1	21.6	16.6	0.8	21.2	1.4	0	12.6	0	3.8	6.6	2.6	0.4

Taxon	13	14	15	16	17	18	19	20	21	22	23	24
Ephemeroptera												
E1	146	232.2	197.2	200.2	377	433.6	327.2	109.2	706	348.4	93.8	309.4
E2	1	8	4	4.4	5.2	12.8	8.2	15.6	16.2	1.8	13.6	19.6
E3	5.4	3.8	13.8	7.2	73.2	4.8	27.4	11	9	27.4	16.4	28.6
E4	0	0	0.8	0	0	0	0	0	0	0	0	0
E5	4.4	3.2	0	0	0	0	0.2	0	0	0	30	4
E6	0.8	0.2	0	0	0	0	0.4	0	0.8	0	0	0
E7	0.2	0	0	0	0.2	0	0	0	0	0	0	0
E8	1.6	0	2	0	0	0	0.2	0	0	0	0	0
Plecoptera												
P1	50.6	32.4	24	11.8	19	1.8	34.8	13.2	0.8	42.8	18.2	10.2
P2	0.2	0	0	0	0.2	0	0	1.2	0	1.4	16	2.8
P3	0	0	0	0	0	0	0	0	0	2	0	5.2
Trichoptera												
TC1	9.6	0.2	0	0	0	0.2	0	0	0	0	0	0
TC2	0	0	0	0	0	0	0	0	1.2	0	0	0.4
TC3	0	0	0	0	0	0	0	0	0.2	2.4	5	0
TC4	0	0	0	0	2.4	0	0	0	0	0.8	1.6	0
TC5	0	0	0	0	0	0	0	0	0	0	2.4	2.4
TC6	0	0	0	0	0	0	0	0	0	0	0	0
TC7	0	0	0	0	0	0	0	0	1.6	0	0	0
TC8	0	0	0	0	0	0	0	0	0.6	0	0	0
TC9	1.6	0	0.2	0	0	0	0	0	0	0	0	0
TC10	0	0	0	0	0	0	0	0	0	0	0	0
TF1	10	3.6	2.4	4.2	10.4	14.2	7	6	7.6	3.2	4.6	6.2
TF2	0	0	0	0	0	0	0	0	0	0	0	0
TF3	6.2	0.6	0.4	1	1.8	0	2.4	2.4	1.2	0	0	0
TF4	0	0.4	0	0	1.6	0	0	0	0	8.4	0	0
TF5	0	0	0	0	0	0	0	0	0	0	0	0.8
TF6	0	0.2	0	0	0	0.2	0	0	0	0	0	0.8
TF7	0.8	1.6	0	0	0	0	0	8.4	0	0	0	0
TF8	0	0	0	0	0	0	0	0	0	0	0	0.2
TN1	27	6.8	14.8	8.8	105.2	13.4	35.8	7.8	0.8	2.2	3.8	2.8

Taxon	1	2	3	4	5	6	7	8	9	10	11	12
Diptera												
D1	83.2	155	50.8	0.8	50.8	6802	32.4	129.4	17	452.8	100.4	91.4
D2	14	7.4	1.6	0	0	0	0.8	0	0	0.4	2.6	0.4
D3	0	0	0	0	0	6.4	0	0	0.2	0	0	0
D4	0	0.8	0	0	0	0	0.8	0	0	0	0	1.6
D5	0.8	0	0.4	0	0.8	0	0	3.2	0.4	10.4	0	0.2
D7	0	0	0	0	0	0.2	0	0	0	0	0	0
D8	0	0	0.8	0	0.2	0	0	0	0	0	0.2	0
D9	0	0	0	0	0	3.2	0	0	0	0	0	0
D10	0	0.8	0	0.8	0	0	0	0	0	0	0	0
D11	0	0	0	0.2	0	0	0	0	0	0	0	0
D12	0	0	0	0	0	0	0	0	0	0	0	0
DC1	10.4	0.2	9.2	1.4	3.2	423.8	0.8	0.2	1.8	1	30.4	0.2
DC2	4	1.6	0	0	0	28.8	3.2	0	1.4	2.2	1.6	0
DC3	0.4	0.8	2.4	0	3.2	4	6	0.2	1.4	2.4	0	1
DC4	6.8	39.2	0.8	5.4	3.2	1111	32.6	0.6	1.8	17	76.2	4.6
DC5	0	0	0	0	0	0	26.4	0	0	0	0	0
DC6	4	4	0	0	4.2	10.4	0.8	0	0.4	0	0	0
DC7	0	0	0	0	0	3.2	0	0	0	0	0.2	0
DC8	0.8	0	0	0.8	0	86.4	0	0	0	3.4	0	0
Coloepoptera												
CA1	18.4	12.6	7.2	8.8	1	0.8	8.6	6.4	23.6	12.4	5.8	14.4
CA2	0.8	0	0.4	0	0	0	2.2	1.8	2.4	0.2	0.6	1.4
CA3	0	0	0	0	0	0	0	0	0	0	0	0
CA4	0	0	0	0	0	0	0	0	0	0	0	0
CA5	0	0.8	0	0	0	0	0	0	0	0	0	0
CL1	0	0	0	0.2	0	0	0.8	0	0.2	4.4	0	0.4
CL2	3.2	1.6	5.6	16.6	0.8	0.8	8	0.6	3.6	9.8	0.8	15.6
CL3	13.6	0	2.4	4.6	0	0	2.8	0.4	0	3.6	0	6.6
CL4	0	0	0	0	0	0	0	0	0	0	0	0
CL5	0	0	0	0	0	0	0.8	0	0	0	0	0
CL6	0	0	0	0.8	0	0	0	0	0	0	0	0

Taxon	13	14	15	16	17	18	19	20	21	22	23	24
Diptera												
D1	73	7.4	31.4	12.8	92.4	4.8	25	20	337.4	391	22.2	20.4
D2	2.6	1.6	7.6	1.8	3.2	0	24.4	1	1.6	0.4	0.2	1.4
D3	0	0	0	0	0	0	0	0	0	0	0	2.6
D4	0	0	0	0	0	0.8	0	0.4	0	0	0	0.8
D5	1	0	0	0	0.2	3.6	0.4	0.6	0	0	0	0
D7	0	0	0	0	0	0	0	0	0.8	0	2.6	0
D8	0	0	0	0	1.2	3.2	0	0	2.4	0.4	0	0
D9	0	0	0	0	0	0	0	0	1.6	0	0	0
D10	0	0	0	0.8	0	0	0	1.2	0	0	0	0
D11	0	0	0	0	0	0	0	0	0	0	0	0.4
D12	0	0	0	0	0	0	0	0	0	0	0.2	0.4
DC1	0	4	0	4.6	8.2	1.6	0	0	2.4	7.6	1.2	4
DC2	1	3.2	1.4	1.2	1.6	0	0.8	0.6	0.8	0.6	6	4.4
DC3	1.2	2.2	2	7.6	0	0	1.2	1.8	9.4	2.4	1.4	1.2
DC4	18.4	27.6	13.2	15	14.4	10.4	12.2	15.4	162.4	16.4	12.6	35.6
DC5	1.6	0	0	0	0	0	0	0	0	0.2	0	0
DC6	0	0	1.6	1.8	0	0.8	0	1.2	6.4	1.4	0	0
DC7	0	2.6	0	0	0	0	0	0	0	0.4	0.2	0
DC8	0.8	0	0	0.2	0	0	0	0	0	6.8	0	4.6
Coloepoptera												
CA1	17.8	16.4	9.8	9.8	13.6	8.8	1.8	6.6	6.6	4.2	8	3.2
CA2	2	2.6	4.2	1.2	1.6	0	2.6	9	0	4.4	5.4	0.8
CA3	0	0	0.8	1.2	0	0	0	0	0	0	0	0
CA4	0	0	0.8	0.2	0	0	0	0	0	0	0	0
CA5	0	0	0	0	0	0	0	0	0	0	0	0
CL1	4.6	1	0	0	2	0	1	1.8	0	0	0	0
CL2	17.6	0.8	5	2.8	24.8	2.4	0.4	1.6	38.4	26.6	5.6	3.2
CL3	0	0	0.4	3.4	12.8	4.4	0	0.6	0	5.2	2.2	26.6
CL4	0	0	0	0	0	0	0	0	1.8	0	0	0
CL5	0	0	0	0	0	0	0	0	0	1.6	0	0
CL6	0	0	0	0	0	0	0	0	0	0	0	0

Taxon	1	2	3	4	5	6	7	8	9	10	11	12
Other												
O1	64	6.2	157.6	14.8	4.4	9.6	0	79.4	57.8	91.6	0	14.4
O2	40.8	2.6	0	1.6	0	160.8	2.4	0	1.2	1	0	0.8
O3	2.8	9.6	0	46.4	0	0	46.8	6.6	0	0.8	0.2	9.8
O4	2	0.6	0	1	0.4	12.8	0.2	5.6	0	1.6	0.8	3
O5	0	0.8	0	0.2	0	3.2	0.8	0	0	0	0	0.8
O6	0.8	0	0	0	0	4.4	0	0.2	0.4	0	0	0
O7	1.2	0	0	0	0	0	0	0.8	0	0	0	0
O8	1.2	0.8	1.6	5.6	1.6	0	0	0.8	0.4	0	0	1.4
O9	0	0	0	0.2	0	0	0.4	0	0	0	0	0
O10	0	0	0	0	0	0	0	0	0	0	0	0
O11	0	0	0	0	0	0	0	0	0	0	0	0
O12	0	0	0	0	0	0	0	0	0	0	0	0
O13	0	0	0	0	0	0	0	0	0	0.8	0	0
O14	0	0.2	0	0	0	0	0	0	0	0	0	0
O15	0	0	0	0	0	0	0	0.2	0	0	0	0
O16	0	0	0	0	0	0	0	0	0	0	0	0

Taxon	13	14	15	16	17	18	19	20	21	22	23	24
Other												
O1	0.8	12	8.4	0.4	59.2	250.4	0.6	44.2	45.8	0	0	10
O2	0	0.8	3.2	2	6.6	3	0	0.2	42	10.4	10.4	22
O3	0	0	22.8	81.8	16.6	3.4	0.6	2.6	0	0	0	0.8
O4	0	0	0	38.8	3.2	20.2	1.8	25.6	0	0	0.2	0.8
O5	0	0	0	0	0	0	0	0	9.6	0	0	0
O6	0	0	0	0	0	0	0	0	7.4	0	0	0.8
O7	0	0	0	0	0.6	0	0	0	0	0	0	0
O8	0.8	0	0	0	9.6	2.6	1.8	2.8	0	0	0	13.4
O9	0	0	0	0	0	0	0	0	0	0	0	0
O10	0	0	0	0.8	0	0	0	0	0	0	0	0
O11	0	0	0	1.8	0	0	0	0	0	0	0	0
O12	0	0	0	0	0	0	0.2	0.8	0	0	0	0
O13	0	0	0	0	0	0	0	0	0	0	0	0
O14	0	0	0	0	0	0	0	0	0	0	0	0
O15	0	0	0	0	0	0	0	0	0	0	0	0
O16	0	0	0	0	0	0	0	0	0	0.2	0	0

Appendix 5: Raw invertebrate data collected from artificial channels in three Hawke's Bay, New Zealand streams, December 2009 (Chapter 6). Values are the pooled number of individuals for the three samples from each channel.

No.	Taxon	EX1.0.C	EX1.0.O	EX1.16.C	EX1.16.O	EX1.8.C	EX1.8.O	EX1.4.C	EX1.4.O
Ephemeroptera									
1	<i>Deleatidium</i> spp.	15	65	51	70	19	32	9	47
2	<i>Zephlebia dentata</i>	0	0	0	0	0	0	0	0
3	<i>Austroclima sepia</i>	1	0	0	0	0	0	0	1
4	<i>Neozephlebia scita</i>	0	0	0	0	1	0	0	2
5	<i>Coloburiscus humeralis</i>	0	0	0	0	1	0	0	1
Trichoptera									
6	<i>Aoteapsyche colonica</i>	42	48	69	48	24	19	18	2
7	<i>Psilochorema</i> A	1	0	0	0	0	0	0	0
8	<i>Hydrobiosis parumbripennis</i>	1	5	0	0	0	1	0	1
9	<i>Hydrobiosis frater</i>	0	1	5	1	0	0	0	0
10	<i>Neurochorema forsteri</i>	0	0	0	4	1	1	0	0
11	<i>Pycnocentria evecta</i>	0	0	0	1	0	0	2	0
12	<i>Pycnocentroides aeris</i>	7	35	16	41	6	64	19	23
13	<i>Olinga feredayi</i>	0	2	0	0	3	0	0	3
14	<i>Helicopsyche poutini</i>	10	1	41	83	14	12	16	44
15	<i>Confluens hamiltoni</i>	0	0	0	0	0	0	0	0
16	<i>Hudsonema amabile</i>	0	0	0	0	0	0	0	0
Diptera									
17	<i>Aphrophila neozelandica</i>	0	0	0	0	0	0	0	0
18	<i>Austrosimulium</i> spp.	0	0	0	0	0	0	1	0
19	Orthocladiinae A	0	2	0	0	0	0	0	0
20	Orthocladiinae B	0	0	0	1	0	2	2	3
21	Orthocladiinae C	0	0	0	0	0	0	0	0
22	Orthocladiinae E	0	0	0	0	0	0	1	1
23	Chironominae A	0	0	0	0	0	0	0	0
24	Chironominae B	0	0	0	0	0	0	0	0
25	Tanypodinae A	0	0	0	0	0	0	0	0
26	<i>Maoridiamesa</i> spp.	0	0	0	0	1	1	0	0
Coleoptera									
27	Elmidae <i>Hydora</i> spp.	0	0	0	0	0	0	0	0
28	Hydraenidae	0	0	0	0	0	0	0	0
Mollusca									
29	<i>Potamopyrgus antipodarum</i>	15	6	19	33	4	0	4	6
30	<i>Physa</i> spp.	0	0	0	0	0	0	0	0
Other									
31	<i>Paracalliope</i> spp.	0	2	1	0	0	0	1	2
32	Platyhelminthes	39	4	58	64	77	16	19	19
33	Oligochaeta	7	4	2	8	0	0	0	2
34	<i>Archichaulioides diversis</i>	0	3	1	0	0	0	0	0

No.	EX2.0.C	EX2.0.O	EX2.16.C	EX2.16.O	EX2.8.C	EX2.8.O	EX2.4.C	EX2.4.O
1	1	6	9	8	16	12	1	17
2	2	0	0	0	0	0	0	0
3	0	0	2	0	0	0	0	0
4	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
6	10	5	0	0	0	0	0	0
7	6	9	3	1	6	2	8	6
8	4	1	1	0	0	8	0	0
9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0
11	8	2	3	1	0	0	0	0
12	26	44	4	17	14	23	18	12
13	0	0	0	0	0	0	4	0
14	0	0	0	0	0	0	0	0
15	0	1	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0
18	2	0	3	0	0	0	0	0
19	0	0	0	0	0	4	0	0
20	12	7	1	3	3	8	21	12
21	2	0	0	0	0	0	4	8
22	0	0	0	0	0	0	0	0
23	1	0	0	0	1	0	0	4
24	0	0	0	2	0	0	0	0
25	0	0	0	0	0	0	8	4
26	0	0	0	0	0	0	0	0
27	3	5	1	1	6	1	0	0
28	0	0	0	0	0	0	0	0
29	78	82	247	182	249	240	306	588
30	0	0	0	0	1	0	1	0
31	0	0	11	0	3	3	51	36
32	2	0	0	1	4	6	5	8
33	5	6	27	13	419	172	55	45
34	0	1	0	0	0	0	0	0

No.	EX3.0.C	EX3.0.O	EX3.16.C	EX3.16.O	EX3.8.C	EX3.8.O	EX3.4.C	EX3.4.O
1	1	8	3	12	6	15	1	5
2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
6	16	0	2	0	0	1	0	0
7	11	6	3	2	4	3	2	6
8	0	0	0	0	0	0	0	0
9	0	0	1	0	0	0	0	0
10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	1
12	13	47	2	47	16	30	16	42
13	0	0	0	0	0	0	1	0
14	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0
16	0	1	0	4	0	1	0	8
17	0	1	0	1	1	1	0	0
18	5	1	4	1	1	0	1	0
19	0	0	0	0	0	0	0	0
20	1	0	0	1	0	2	1	3
21	0	0	0	0	0	1	1	0
22	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0
28	0	0	0	1	0	0	0	0
29	25	57	89	122	49	94	15	158
30	0	0	0	0	0	0	0	0
31	0	0	0	4	2	2	1	4
32	4	0	0	1	2	0	0	0
33	16	7	11	20	38	24	17	28
34	0	0	0	0	0	0	0	0

Appendix 6: Reprint of co-authored paper in New Zealand Journal of Ecology.

Collier, K. J., B. Aldridge, B. J. Hicks, J. Kelly, A. Macdonald, B. J. Smith, and J. Tonkin. 2009. Ecological values of Hamilton urban streams (North Island, New Zealand): constraints and opportunities for restoration. *New Zealand Journal of Ecology* **33**:177-189.

Available on-line at: <http://www.newzealandecology.org/nzje/>

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Ecological values of Hamilton urban streams (North Island, New Zealand): constraints and opportunities for restoration

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Published on-line: 3 July 2009

Abstract: Urban streams globally are characterised by degraded habitat conditions and low aquatic biodiversity, but are increasingly becoming the focus of restoration activities. We investigated habitat quality, ecological function, and fish and macroinvertebrate community composition of gully streams in Hamilton City, New Zealand, and compared these with a selection of periurban sites surrounded by rural land. A similar complement of fish species was found at urban and periurban sites, including two threatened species, with only one introduced fish widespread (*Gambusia affinis*). Stream macroinvertebrate community metrics indicated low ecological condition at most urban and periurban sites, but highlighted the presence of one high value urban site with a fauna dominated by sensitive taxa. Light-trapping around seepages in city gullies revealed the presence of several caddisfly species normally associated with native forest, suggesting that seepage habitats can provide important refugia for some aquatic insects in urban environments. Qualitative measures of stream habitat were not significantly different between urban and periurban sites, but urban streams had significantly lower hydraulic function and higher biogeochemical function than periurban streams. These functional differences are thought to reflect, respectively, (1) the combined effects of channel modification and stormwater hydrology, and (2) the influence of riparian vegetation providing shade and enhancing habitat in streams. Significant relationships between some macroinvertebrate community metrics and riparian vegetation buffering and bank protection suggest that riparian enhancement may have beneficial ecological outcomes in some urban streams. Other actions that may contribute to urban stream restoration goals include an integrated catchment approach to resolving fish passage issues, active reintroduction of wood to streams to enhance cover and habitat heterogeneity, and seeding of depauperate streams with native migratory fish to help initiate natural recolonisation.

Keywords: biodiversity; fish; functional value; impervious surface; invertebrates; seepage

Introduction

Urbanisation has homogenised otherwise heterogeneous physical environments, and replaced often diverse native flora and fauna with a variety of common urban-adapted species dominated by exotic taxa (McKinney 2005). Recently, interest has accelerated in ecological restoration of urban areas given that cities are where most people interact with native biodiversity most often. For urban streams, however, ecological rehabilitation can be problematic because of the overriding influence of stormwater on stream ecology (Bernhardt & Palmer

2007). Stream channels in cities are typically used to convey stormwater out of the urban environment as rapidly and efficiently as possible to avoid flooding and erosion, and catchments with impervious area as low as 10% can have significantly impaired aquatic macroinvertebrate communities (Walsh 2004). Indeed, the term 'urban stream syndrome' has been coined to describe the state of ecological degradation consistently observed in urban streams (Meyer et al. 2005).

Because stormwater enters streams directly via pipes, rather than naturally through overland flow and subsurface drainage, it significantly alters the hydrology

New Zealand Journal of Ecology (2009) 33(2): 177-189 ©New Zealand Ecological Society

of urban streams leading to more frequent floods, rapidly changing hydrographs, and higher peak flows (Walsh et al. 2005a). The erosive forces generated by this altered hydrology can cause channel incision and bank erosion, elevating fine sediment levels and resulting in increased water turbidity and smothering of streambed habitats (Chin 2006). Stormwater flushes can also increase water temperatures significantly and elevate concentrations of nutrients and a wide range of contaminants in streams (Walsh et al. 2005a). The desire for hydraulic efficiency has led to the piping or reconfiguration of many stream channels, and the reinforcement of stream banks and beds. In addition, stream channels are often cleared of aquatic plants and wood, and vegetation in riparian areas may be controlled to facilitate the rapid movement of floodwaters downstream. All these changes alter ecosystem function and influence the composition of biological communities in urban streams that are typically characterised by low diversity, few sensitive species and dominance by tolerant taxa (Meyer et al. 2005).

Roy et al. (2006) proposed that stream restoration in urban catchments should focus on the catchment drainage system rather than instream or riparian habitat. Improved drainage design can reduce the proportion of impervious area directly connected to streams through stormwater pipes by maximising runoff detention, infiltration and off-channel retention of water (Taylor et al. 2004; Walsh 2004; Walsh et al. 2005b). Appropriate technology can be implemented with relative ease in many new developments, but there are obvious difficulties and costs associated with retrospectively disconnecting stormwater systems to reduce effective impervious area in existing urban areas. Current attempts to restore natural vegetation sequences and foster native terrestrial biodiversity in the gullies of Hamilton City, New Zealand, have highlighted the potential to link terrestrial restoration with the protection and enhancement of aquatic values. In this paper we (1) compare selected attributes of urban streams (fish distribution, macroinvertebrate communities, habitat, and biogeochemical and hydraulic function) with periurban sites on the outskirts of Hamilton City, and (2) explore environmental factors associated with aquatic species' distribution in this urban environment. Based on the results of this work and other published studies, we discuss potential constraints and opportunities for urban stream restoration in Hamilton City.

Study area

Hamilton is New Zealand's seventh most populous city, with 185 000 inhabitants (2005 figures, www.stats.govt.nz). The Waikato River bisects the city, where its median discharge is $254 \text{ m}^3 \text{ s}^{-1}$ (Environment Waikato, unpubl. data). Around 15 000 years ago, the river entered a period of downcutting, and as it deepened springs were exposed along the banks. These springs gradually undermined the riverbanks, and in a process known as spring sapping

caused erosion of adjacent underlying sand, silt, peat and gravel, eventually creating gully streams that now flow through the city into the Waikato River (McCraw 2000). There are four major gully systems in Hamilton City (Kirikiriroa, Mangakotukutuku, Te Awa o Katapaki, and Waitawhiriwhiri) with numerous minor systems (Fig. 1), collectively occupying around 750 ha or 8% of the city area (Downs et al. 2000). Gully floor vegetation is frequently dominated by the deciduous exotic grey willow (*Salix cinerea* L.), though beneath this can be an understorey of indigenous plants including ground ferns, māhoe (*Meliccytus ramiflorus* J.R.Forst. & G.Forst.) and cabbage trees (*Cordyline australis* (G.Forst.)Endl.).

Hamilton City gullies accommodate around 120 km of stream distinguished at the 1:50 000 mapping scale (Environment Waikato, unpubl. data). In addition, there is an unknown length of unmapped small stream channels, some of which now flow in pipes, as well as many springs and seepages. The larger streams originate in low-gradient agricultural catchments on the outskirts of the city, although some smaller streams have catchments that are entirely urbanised. In established urban areas, most impervious land appears to be highly connected to the stormwater network, which pipes stormflows directly into streams. The percentage of upstream catchment area with impervious surfaces can range from <5% for streams with most of their catchment still in rural land, to around 70% in some industrial suburbs (Environment Waikato, unpubl. data).

Methods

Study sites

A total of 56 sites was included in this study, comprising 28 urban streams, 19 periurban streams, and 9 urban seepages (Appendix 1; Fig. 1). Urban sites had residential or industrial development adjacent to them, although typically it did not extend to the stream edge due to the presence of parks and gullies. Periurban sites were surrounded by rural land (mostly farms and lifestyle blocks) at the time of sampling; rural land use dominated upstream catchments, although some periurban sites had residential development within their catchments (e.g. S1, S2). Of the streams sampled, 40 were assessed for fish occurrence, 33 for stream invertebrate community composition and habitat quality, and 28 for biogeochemical and hydraulic function. The seepages were sampled for adult caddisflies (Trichoptera) only. Fish, invertebrates and functional values were all assessed at 22 sites, and fish sampling only was conducted at 12 sites. Stream sampling reach lengths were 50–100 m, with all attributes measured in the same reach unless otherwise indicated (see Appendix 1; Fig. 1).

Channel widths ranged from 0.4 to 7 m but were similar on average at urban and periurban sites (Table 1).

Table 1. Physicochemical attributes of sampling sites in urban ($n = 28$) and periurban ($n = 19$) Hamilton City. Single measurements were made per site during daylight hours in 2005–2007 (Environment Waikato, unpubl. data).

	Urban				Periurban			
	Mean	SE	Min	Max	Mean	SE	Min	Max
Active channel width (m)	1.9	0.2	0.4	5.0	2.4	0.4	0.3	7.0
Sand/silt/clay (%)	71.5	4.6	10.0	100.0	84.5	5.2	10.0	100.0
Gravel-cobble (%)	26.9	4.3	0.0	90.0	12.4	3.3	0.0	50.0
Water temperature ($^{\circ}\text{C}$)	18.0	0.4	15.3	24.0	18.6	0.4	16.2	22.8
Dissolved oxygen (%)	80.4	2.7	48.0	104.4	78.1	5.0	43.0	122.2
Dissolved oxygen (mg L^{-1})	10.2	2.6	4.7	79.4	7.3	0.5	4.1	11.0
pH	7.3	0.1	6.4	7.8	7.0	0.1	6.4	7.5
Conductivity ($\mu\text{S cm}^{-1}$ @ 25°C)	198.8	20.1	55.1	673.0	219.6	9.3	123.3	302.1

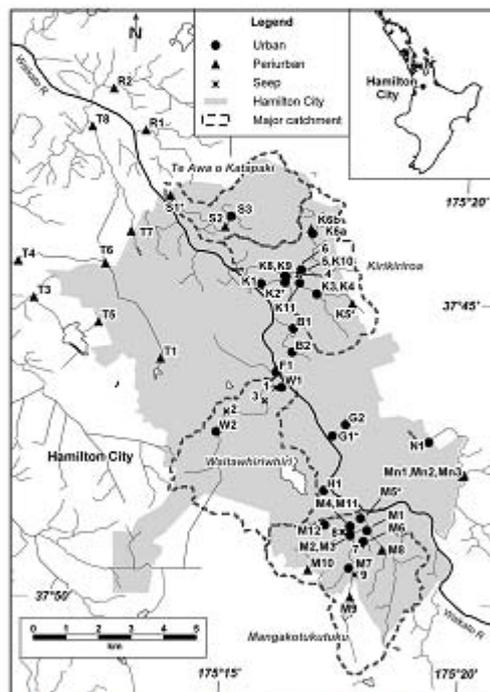


Figure 1. Map of sampling sites showing boundaries of the city and major catchments. * = fish and invertebrate sampling sites >100 m apart. See Appendix 1 for further details.

The percentage of fine substrates (sand, silt and clay) on the streambed was high at all sites (>70%), but significantly greater in periurban streams (Mann–Whitney $U = 356$, $d.f. = 1$, $P < 0.05$). This difference most likely reflected the higher gradient of urban streams as they approach the Waikato River, and the introduction of rocks to stabilise bank erosion which presumably contributed to

gravel/cobble substrates in urban streams. Measured spot water temperatures did not exceed 24°C , and dissolved oxygen saturation was similar in urban and periurban streams (means = 80 and 78%, respectively), although low oxygen concentrations (<5 mg/L) were measured at some sites (Table 1). pH was circumneutral in both urban and periurban streams, but conductivity was significantly higher at periurban sites ($U = 382$, $d.f. = 1$, $P < 0.05$), potentially reflecting enrichment from agricultural development.

Fish

Fish were collected at 24 urban and 16 periurban sites between December 2005 and March 2006 (Appendix 1; Fig. 1). Five Gee minnow traps (5-mm mesh) were set at each site, and a fyke net (25-mm mesh) was also set if the water was deeper than about 1 m (13 sites; Appendix 1). A perforated container of cat biscuits was attached within each trap and net as an attractant. Streams with sufficiently clear water ($n = 13$) were also spotlighted at night, and 10 shallow sites with suitable access were electric fished using a backpack electrofishing machine (EMF 300, NIWA Instrument Systems, Christchurch). Three methods (minnow traps or fyke nets, electric fishing and spotlighting) were conducted together at eight sites (Appendix 1).

Macroinvertebrates

Of the 35 stream sites sampled for invertebrates, 25 were surrounded by urban development, and 10 were in periurban settings (Appendix 1; Fig. 1). Stream macroinvertebrates were collected from stable habitats in flowing water using a D-frame net (0.5-mm mesh) between December 2005 and January 2006 (see Collier & Kelly 2005). Collection involved kicking loose gravel-cobble substrate in front of the net, hand-brushing embedded substrate elements and wood, and jabbing the net in among macrophytes and along stream edges with a similar amount of effort at all sites. The resulting samples were preserved in c. 70% isopropanol, and were

later processed by identifying at least 200 invertebrates (excluding pupae) from randomly selected subsamples, followed by a search for unrecorded taxa in the rest of each sample. Subsampling was achieved by dividing the processing tray into a grid and randomly selecting one cell for processing; additional cells were added until the desired number of macroinvertebrates was obtained with all animals in the final cell being removed. This process yielded an average of 213 individuals per site, with only one sample (G1) not reaching 200 individuals.

Identifications were based on Winterbourn et al. (2000) (insects), Winterbourn (1973) (molluscs), and Chapman & Lewis (1976) (crustaceans). The level of taxonomic resolution was genera for most insects and molluscs, and ranged from family to phylum for other groups, as recommended by Stark et al. (2001) for stream environmental monitoring in New Zealand. The total number of taxa, and the number of taxa and percentage abundance of sensitive Ephemeroptera, Plecoptera, and Trichoptera excluding Hydroptilidae (denoted as EPT*), were calculated from the macroinvertebrate data. Hydroptilidae was excluded because some species can proliferate among growths of filamentous algae, which are often typical of degraded conditions. In addition, the Macroinvertebrate Community Index (MCI) was calculated as described in Stark et al. (2001), and the Urban Community Index (UCI), which may be a more appropriate index for discriminating ecological conditions among streams that lacked sensitive species but were impacted by urban development, was calculated following Suren et al. (1998, unpubl. report) and Boothroyd & Stark (2000). The UCI uses Canonical Correspondence scores for taxa from a nationwide urban stream survey as tolerance values to weight species occurrence. These weighted values are then aggregated to provide the UCI. It was necessary to combine taxa belonging to *Zephlebia* and *Neozephlebia*, and *Orthopsyche* and *Aoteapsyche*, because not all taxa found in the present study were part of the original UCI dataset. Higher EPT*, MCI and UCI scores indicate better ecological condition.

Adult Trichoptera

Ultraviolet light traps were used to attract adult Trichoptera around seepages at three urban sites in each of the Mangakotukutuku, Kirikiriroa, and Waitawhiriwhiri catchments (total of nine sites). These catchments represented a gradient of urbanisation intensity, with the Mangakotukutuku having a significant proportion of its catchment outside the city, Waitawhiriwhiri with a high level of industrial land, and Kirikiriroa intermediate and characterised by more recent high density urban development. Each light trap consisted of a low power (6 W) model F6T5 blacklight fluorescent tube laid over a white dish (38 × 27 × 6 cm). The dish was half-filled with water into which a few drops of detergent had been mixed to break the water surface tension. The lights were powered

by 12-volt batteries run from timing units that enabled all lights to be turned on and off, simultaneously. Light traps were set to run from 2100 to 2300 hours and 0200 to 0300 hours at all sites on the same night each month from November 2006 to January 2007. Samples were preserved in isopropanol and Trichoptera were later identified under a binocular microscope using Neboiss (1986) and Smith & Ward (unpubl. key to adult Trichoptera).

Habitat assessment

Habitat assessments were made at all sites where stream invertebrates were collected (Appendix 1), using the method described by Collier & Kelly (2005). This procedure provides an integrative score for riparian, bank, channel and instream conditions by visually evaluating nine attributes on a scale of 1 (lowest habitat value) to 20 (highest habitat value), with possible total scores ranging from 9 to 180 (see Results Fig. 5 for component attributes). Riparian zone buffering refers to the buffering from the adjacent land use provided by riparian vegetation; for example, grass next to a city stream would provide buffering from urban land, but it would not provide buffering from agriculture.

Stream Ecological Valuation (SEV)

Hydraulic and biogeochemical components of the SEV methodology (see Rowe et al. 2008, in press) were assessed at five periurban and 23 urban sites (Appendix 1; Fig. 1). Hydraulic functions included natural flow regime, connectivity to floodplain, connectivity for species migrations, and connectivity to groundwater. Biogeochemical functions included water temperature control, dissolved oxygen concentrations, organic matter input, instream particle retention, decontamination of pollutants, and floodplain particle retention. The SEV methodology involves measuring (at 10 cross-sections) or scoring (visually along the sampling reach) selected attributes, and then integrating them using algorithms that express the ability of the stream to perform certain ecological functions. Algorithms were developed by an expert panel and were tested on a range of urban streams in Auckland City (Rowe et al. 2008, in press). The outputs from these algorithms were aggregated relative to native forest reference conditions to provide an overall score for each function with a potential value between 0 and 1, with higher scores indicating greater similarity to the reference condition. The reference site used for this purpose was the closest native forest stream, located in the Hakarimata Ranges 11 km to the north-west of Hamilton City (NF in Quinn et al. 1997). Details of the field methodology for the SEV components are provided in Rowe et al. (2008).

Statistical analysis

Non-parametric tests were used for all statistical analyses because of the skewed nature of most of the

data. Differences between urban and periurban sites for macroinvertebrate metrics, habitat scores, and SEV biogeochemical and hydraulic functions were assessed using Mann–Whitney U tests, whereas differences among urban catchment groupings (Kirikiriroa, Mangakotukutuku, other catchments combined) were assessed using Kruskal–Wallis tests. Relationships between macroinvertebrate metrics and habitat and SEV scores were explored using Spearman rank correlations. Fish catch data were not analysed statistically because various levels of effort were used at different sites depending on habitat characteristics.

Results

Distribution of fish

With the exception of juvenile galaxiids and torrentfish, a similar complement of fish species was found in urban and periurban settings (Fig. 2). Altogether, eight species of native fish and four species of introduced fish were caught in and around Hamilton City. The native fauna comprised the shortfin eel (*Anguilla australis* Richardson 1848), the longfin eel (*A. dieffenbachii* Gray 1842), banded kōkopu (*Galaxias fasciatus* Gray 1842), giant kōkopu (*G. argenteus* (Gimelin 1789)), inanga (*G. maculatus* (Jenyns 1842)), common smelt (*Retropinna retropinna* (Richardson 1848)), common bully (*Gobiomorphus cotidianus* McDowall 1975), and torrentfish (*Cheimarrichthys fosteri* Haast 1874). The latter was only found in a fast-flowing, stony section of one urban stream. The introduced koi carp (*Cyprinus carpio* Linnaeus 1758), gambusia (*Gambusia affinis* (Baird & Girard 1854)), catfish (*Amieurus nebulosus* Le Sueur 1819) and indeterminate trout were also caught in Hamilton urban streams. However, only gambusia, which was found at over a quarter of the sites sampled, was widespread (Fig. 2). Shortfin eel (61% of sites) and longfin eel (34%) were the most widespread species

collected. Smelt, banded kōkopu, giant kōkopu and unidentified whitebait (juvenile Galaxiidae) were found at 2–6 sites within the city (Fig. 2). Catfish were found at only one periurban site, although they have been seen subsequently within the city in Waitawhiriwhiri Stream (JK, pers. obs.).

Stream macroinvertebrates

Macroinvertebrate communities of Hamilton's urban streams were dominated by tolerant species including *Potamopyrgus antipodarum* (31% of numbers across all urban sites), Oligochaeta (26%) and Chironomidae (21%). The freshwater crayfish/kōura (*Paranephrops planifrons*) was not caught in traps or nets at any site but was found at two urban and two periurban sites during electric fishing (Fig. 2). Median numbers of macroinvertebrate taxa per sample (taxa richness) and sensitive EPT* taxa were similar at urban and periurban sites (Fig. 3A, B). The typical urban and periurban site supported low %EPT* (median <2%; Fig. 3C), although there was considerable variability among sites, especially in EPT* taxa richness. The Mangakotukutuku samples included one urban site (with a predominantly gravel streambed) and one periurban site (characterised by soft bed sediments and willow roots) that had particularly diverse or abundant EPT faunas relative to other sites. Statistical comparisons of metrics indicated no significant difference between urban and periurban sites ($U = 91$ for both EPT* metrics, d.f. = 1, $P > 0.05$), but within the urban sites EPT* taxa richness was significantly higher in the Mangakotukutuku catchment (Kruskal–Wallis $H = 9.1$, d.f. = 2, $P < 0.05$).

Median MCI values for site groupings ranged from 68 to 74 at the periurban and urban sites (Fig. 3D) and ranges were indicative of poor to good stream quality (Wright-Stow & Winterbourn 2003). UCI values were more variable for urban than periurban streams (Fig. 3E) and no statistically significant differences were detected for either index between the two groups of sites (Mann–Whitney $U = 63$ and 84, respectively, d.f. = 1, $P > 0.05$) (Fig. 3);

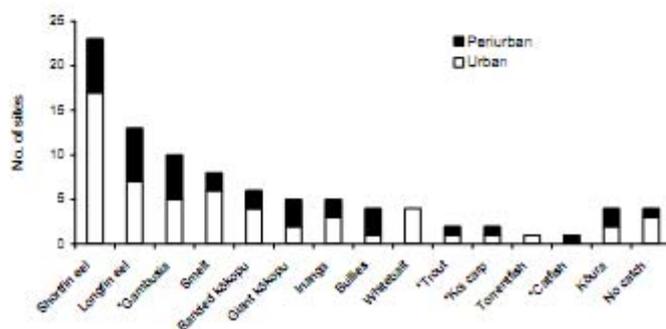


Figure 2. Number of sites where different fish species and freshwater crayfish (kōura) were caught during a survey of 24 urban and 16 periurban stream sites in and around Hamilton City. Whitebait includes all unidentified juvenile galaxiids and trout were not identified to species. * = introduced species

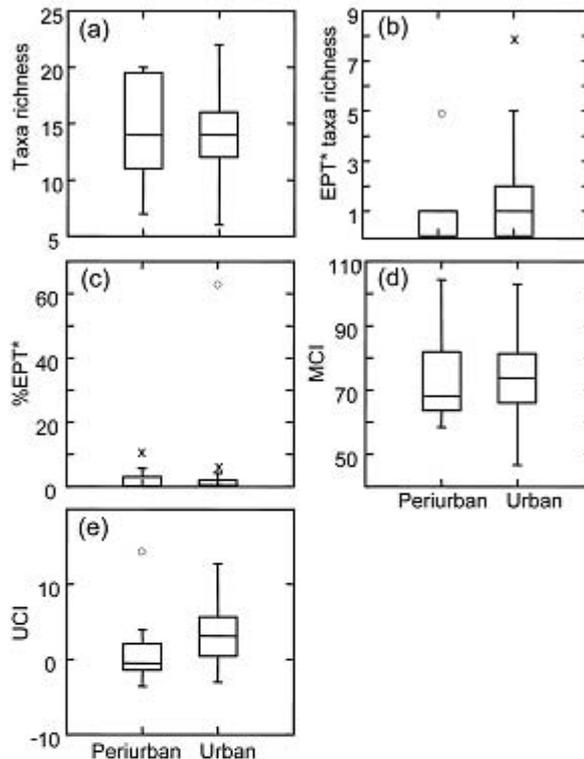


Figure 3. Box plots illustrating: A, total numbers of macroinvertebrate taxa (taxa richness); B, the number of Ephemeroptera, Plecoptera and Trichoptera (excluding Hydroptilidae) taxa (EPT* taxa richness); C, percentage EPT* abundance; D, the Macroinvertebrate Community Index (MCI); and E, the Urban Community Index (UCI) in periurban ($n = 8$) and urban ($n = 25$) sites. Horizontal lines = median; box = interquartile range; crosses and circles = outliers and extreme outliers, respectively.

however, there were differences between urban catchments ($H = 8.1$, $d.f. = 2$, $P < 0.05$) with UCI scores being highest in the Mangakotukutuku.

Adult Trichoptera faunas

In all, 1710 adult Trichoptera representing seven families and 23 species were collected in light traps around urban seepages (see Smith (2007) for species list). This contrasts with only three trichopteran taxa found in larval collections from streams near the light-trapping sites, and 10 larval taxa found across all stream macroinvertebrate sampling sites. Hydrobiosidae, represented by three genera and six species, was the most diverse family caught in light traps. Richness of adults (mean number of species per site) was greatest for the Mangakotukutuku Stream (13 species), followed by the more developed Kirikiriroa catchment (11 species), and the highly developed Waitawhiriwhiri catchment (6 species). The caddisfly catch included one previously undescribed species, the microcaddisfly *Oxyethira kirikiriroa* (Smith 2008), which was one of five species caught only at the Kirikiriroa seepages. The other four were *Aoteapsyche colonica*, *Hydrobiosis budgei*,

H. umbripennis and *Pycnocentria funerea*. *Pycnocentrodus aeris* was only caught adjacent to Waitawhiriwhiri seepages, whereas *Orthopsyche thomasi* was only recorded from light traps set in the Mangakotukutuku seepages. Of the Trichoptera species collected, *Edpercivalia thomasoni*, *O. thomasi*, *Triplectidina moselyi* and *Pseudoeconesus histirpis* are generally considered obligate forest species, and along with *Polyplectropus altera* and *P. aurifusca* indicate the presence of seepages or small stream habitats (B. Smith, unpubl. data).

Kirikiriroa light trap samples contained the greatest number of adult aquatic insects (1210), whereas the Waitawhiriwhiri and Mangakotukutuku traps produced similar numbers of individuals (260 and 240, respectively). Over half the species caught were represented by five or fewer individuals. Adults of the net-spinning Hydropsychidae (mainly *Aoteapsyche winterbourni*) were the most commonly caught, comprising 66% of total numbers. Hydropsychidae dominated adult Trichoptera catches at the Kirikiriroa and Waitawhiriwhiri sites, but relative abundances were similar across five families at the Mangakotukutuku sites (Fig. 4). Overall, the six species indicative of native forest seepages and small streams

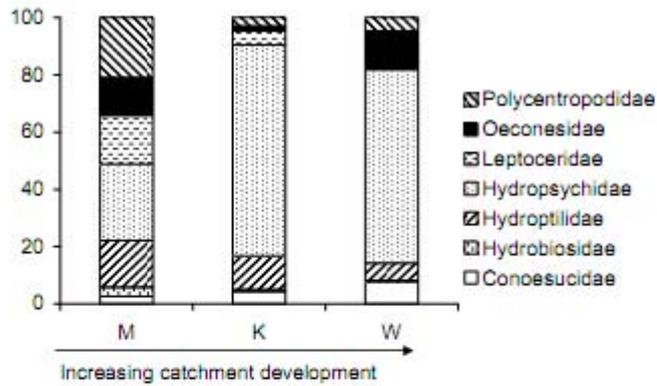


Figure 4. Percentage composition of Trichoptera families collected in light traps adjacent to urban seepages in three catchments (three sites combined per catchment) (see Fig. 1). M = Mangakotukutuku; K = Kirikiriroa; W = Waitawhiriwhiri.

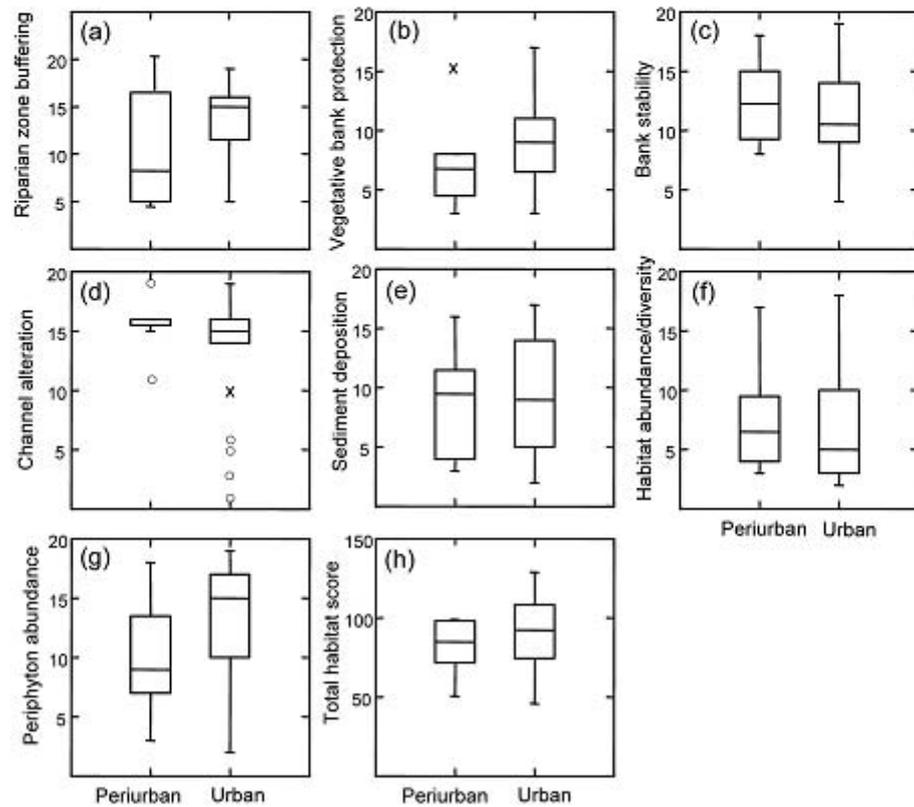


Figure 5. Box plots illustrating: A-G, scores for habitat quality components (ranges 1–20); and H, total score (sum of all components) for periurban ($n = 10$) and urban ($n = 25$) sites. Conventions as in Fig. 3.

represented 4.5%, 17.7% and 40.0% of total numbers in the Kirikiriroa, Waitawhiriwhiri and Mangakotukutuku sites, respectively. The relative abundance of trichopteran families did not appear to be directly related to degree of catchment development, although they were more evenly represented in the least developed catchment (Fig. 4).

Habitat

Riparian vegetation typically provided greater buffering from adjacent land use at urban than periurban sites (Fig. 5A), although variability within periurban sites was high, reflecting the occasional presence of willows and other trees that buffered streams from adjacent agricultural land. Nevertheless, median values for vegetative bank protection and bank stability were similar (7–9 and 11–12, respectively; Fig. 5B, C), as were other habitat components and the total scores (Fig. 5D–H). Within the urban sites (i.e. excluding periurban sites), total habitat score was significantly correlated with %EPT* ($r_s = 0.44$, $P < 0.05$, $n = 25$), and riparian buffering was correlated with EPT* taxa richness ($r_s = 0.54$, $P < 0.01$) and %EPT* ($r_s = 0.49$, $P < 0.05$). Similarly, MCI was significantly correlated with riparian buffering ($r_s = 0.48$, $P < 0.05$), and with degree of channel alteration ($r_s = 0.48$, $P < 0.05$). The UCI was significantly correlated with vegetative bank protection ($r_s = 0.46$, $P < 0.05$). Collectively, these relationships infer a positive association between the extent and vigour of riparian buffer zones, channel integrity, and the condition of macroinvertebrate communities in urban streams.

Hydraulic and biogeochemical components of the SEV

Stream Ecological Valuation analysis indicated that the median hydraulic function score was 0.78 for periurban sites and 0.72 for urban sites relative to the native forest reference condition, whereas biogeochemical function scores were 0.58 and 0.73, respectively (Fig. 6). Urban sites had significantly lower hydraulic function ($U = 94$, d.f. = 1, $P < 0.05$) and higher biogeochemical function ($U = 26$, d.f. = 1, $P = 0.05$) than periurban sites (Fig. 6). However, significant differences were not observed within urban catchments ($H = 0.6$ and 0.8 for hydraulic and biogeochemical function, respectively; d.f. = 2, $P > 0.05$). These functional values were not significantly correlated with any of the invertebrate metrics evaluated for urban sites.

Discussion

Urban stream values

Despite the well-documented effects of stormwater runoff, urban streams in Hamilton City appear to provide similar overall habitat quality to periurban streams and support a similar range of fish species. Indeed, two of the species

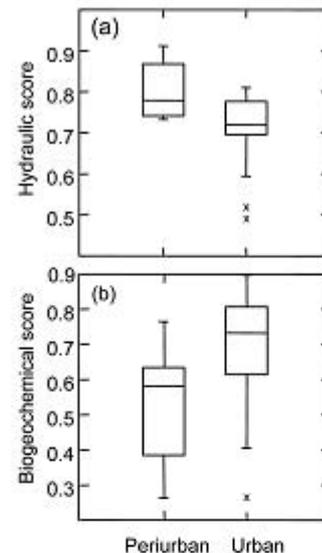


Figure 6. Box plots illustrating: A, hydraulic function; and B, biogeochemical function for periurban ($n = 5$) and urban ($n = 23$) sites following Rowe et al. (2008). Each function is expressed as a ratio of that measured at a native forest reference site, with higher scores indicating greater similarity to the reference condition. Conventions as in Fig. 3.

recorded in city streams, longfin eel and giant kōkopu, are considered threatened and are in gradual decline (Hitchmough 2005). Some native fish species may be able to persist in urbanised catchments because of the availability of cover to provide refugia from stormwater flows. For example, giant kōkopu are often found associated with overhanging riparian vegetation and instream cover such as that provided by accumulations of wood and undercut banks (Bonnett et al. 2002; Baker & Smith 2007), and banded kōkopu prefer small streams with abundant cover (Rowe & Smith 2003). The ability of several galaxiid species to acquire significant proportions of their nutrition from terrestrial insects that fall into streams (e.g. Hicks 1997) may enable some species to survive in urban environments with depauperate instream food supplies.

The macroinvertebrate communities of most streams in Hamilton City were generally comparable with urban settings elsewhere in being dominated by taxa that are tolerant of moderately poor water quality and habitat conditions (Blakely & Harding 2005; Suren & McMurtrie 2005; Walsh et al. 2005a). Communities in most periurban streams were also characterised by tolerant taxa, suggesting that upstream land use could partly influence the composition of communities

occurring in downstream urban settings, although direct comparisons were complicated by physicochemical differences between periurban and urban sites (Table 1). Nevertheless, macroinvertebrate communities at one urban site with a low level of upstream development on the Mangakotukutuku Stream formed a clear outlier in terms of macroinvertebrate metrics, highlighting that broad-scale ecological knowledge is required to identify high-value sites that persist within urban environments.

Seepage habitats that are disconnected from the stormwater network harboured around 30% of the caddisfly diversity known from Hamilton City (BJS, unpubl. data), underscoring the role these often small and overlooked habitats can play in maintaining urban biodiversity values. A combination of soft benthic sediments, shade offered by low-growing riparian grasses, and ample food resources (leaves and small sticks) may enable caddisfly species typical of forested settings to persist in urban seepages. The retention of vegetated gully systems throughout Hamilton City seems to have protected many seepage habitats as part of the riparian complex. Our results suggest that local aquatic biodiversity may be higher where extensive vegetated riparian areas and natural groundwater flows interact than where development and drainage occur to the stream edge.

Constraints to urban stream restoration

Hydraulic functions such as maintenance of a natural flow regime and retention of connectivity to the floodplain appear to be constrained in urban settings, most likely reflecting the combined effects of channel modification and stormwater hydrology. In contrast, biogeochemical function was enhanced in urban streams relative to periurban environments because riparian vegetation provided shade, potential food supplies and habitat in gully streams. Hydrology also appeared to constrain the diversity of urban stream macroinvertebrate communities, which showed a marked decline in the richness of sensitive macroinvertebrate taxa when upstream impervious area exceeded around 10% (KJC, unpubl. data), consistent with the findings of Walsh (2004) who concluded that factors associated with stormwater connection limit the ecological potential of stream macroinvertebrate communities in urban settings. As well as stormwater effects, iron deposition and associated bacterial growths are extensive in several of Hamilton's urban streams (KJC, pers. obs.), reflecting inputs of iron-rich groundwater. Growth associated with such inputs are known to limit stream macroinvertebrate communities (Wellnitz et al. 1990).

Freshwater crayfish are rarely encountered in Hamilton streams, although they can be common and achieve relatively high biomass in nearby pasture streams (Parkyn et al. 2002). Similarly, the migratory shrimp *Paratya curvirostris* was notably absent from urban stream samples obtained as part of this study, despite shrimps

having been seen in a Mangakotukutuku tributary with low upstream impervious area (BMTAA, pers. obs.) and in the nearby Waikato River. The reason for the poor representation of large Crustacea in urban streams is unclear, but it may partly relate to high susceptibility to contaminants carried in stormwater and accumulating on sediments where they live (crayfish) or feed (shrimp), or barriers to the movement of migratory shrimps (e.g. Resh 2005).

Assessment of the severity of passage impedance to upstream migrating fish at 45 road crossings in Hamilton City indicated that 42% of culverts were likely to prevent upstream passage at most flows or low flows (Aldridge & Hicks 2006). The frequency of passage restrictions in urban streams reflects the high density of roading and suggests that culverts have the potential to be major modifiers of the distribution of native diadromous fish (and shrimps where other conditions allow) in cities. Thus, impediments to passage need to be addressed before physical habitat restoration to ensure the long-term sustainability of migratory populations. An important factor when considering culvert remediation work is the potential risk of enhancing access for troublesome exotic species, such as koi carp and catfish, which our survey indicated were not currently widespread in Hamilton City streams. Work in Christchurch urban streams has suggested that road culverts could also act as partial barriers to upstream flight of insects, with potential consequences for larval recruitment in restored sections of stream (Blakely et al. 2006).

Opportunities for urban stream restoration

A key forerunner to establishing restoration priorities is the identification and protection of existing high-value sites so they do not become further degraded. As demonstrated in our study, high-value aquatic sites can persist within cities despite the varied effects of urbanisation on water quality, fish passage, habitat, and hydrology. Seepage habitats were associated with high biodiversity of adult caddisflies, and likely also harbour a range of other wetland species. For example, the giant bush dragonfly *Uropetala carovei*, occasionally seen around Hamilton City, spends 5–6 years living in wetland burrows (Rowe 1987). Similarly, streams with low stormwater connectivity may harbour comparatively healthy macroinvertebrate communities and warrant protection to ensure these values are retained. Given these potential sources of colonists present within Hamilton City, connectivity is unlikely to be a concern for stream insect recolonisation, as in Christchurch for example (Suren & McMurtrie 2005). These findings underscore the importance of maintaining the disconnection from stormwater of high-value streams and seepages in urban environments and areas proposed for development.

Our results point to a positive association between riparian buffering and macroinvertebrate metrics,

suggesting that riparian planting may enhance the distribution and abundance of some moderately sensitive taxa in urban streams. Furthermore, riparian planting may enhance some of the biogeochemical functions of urban streams, such as water temperature regulation through shading, and by promoting organic matter inputs and particle retention. It has also been suggested that improving instream habitat quality, for example through riparian planting, may reduce the abundance of some nuisance introduced species such as gambusia (Ling 2004). However, development of riparian shade can decrease grass growth on streambanks and destabilise deposited sediments, leading to channel widening as a shaded-channel morphology re-establishes (Davies-Colley 1997; Collier et al. 2001). This phenomenon has been documented in small Waikato pasture streams, but it is not clear to what extent it would occur along urban streams following riparian planting because altered hydrology due to stormwater runoff is likely to modify the process.

The development of riparian forest is also likely to lead to natural recruitment of large wood to streams in due course. Large, stable pieces of wood in the stream channel are increasingly being recognised for their role in creating more diverse instream habitats, providing cover for fish, and serving as a substrate for macroinvertebrates where bed sediments are unstable (Hildebrand et al. 1998; Collier & Halliday 2000; Gerhard & Reich 2000; Bonnett et al. 2002). Stable wood in channels and rigid riparian plant stems can impede water flow during floods, thereby reducing hydraulic stress on instream biota and leading to lower but extended flood peaks and longer periods of localised flooding (Collier et al. 1995). This may benefit species such as eels, which are known to follow rising water levels during floods, allowing them to use inundated areas as supplementary feeding habitat (Jowett & Richardson 1994). However, the timescale required to achieve natural wood recruitment from native trees is considerable (Meleason & Hall 2005). This time factor, coupled with the need to protect downstream infrastructure and property, suggests that managed introductions would be required if large wood were to be used as a habitat restoration option in urban streams.

Restoration goals for urban streams may differ for macroinvertebrate and native fish communities because of their apparently different susceptibilities to stormwater inputs. Although some native fish species appear to be resilient to urban development, it is difficult to restore the natural structure of fish communities at urban sites because of the varied combination of local and downstream factors that regulate fish distribution and abundance. Thus, rather than striving for natural fish community structure, a more attainable goal may be to enhance the distribution and abundance of iconic native species (e.g. large galaxiids) by identifying the specific aspects of their habitat and biology that constrain populations. Recent work in Hamilton urban streams has highlighted the potential for

actively introducing naïve farm-reared giant kōkopu into sites where natural recruitment may be limited (Aldridge 2008). These farm-reared giant kōkopu grew rapidly (up to 0.11 g per day) in urban streams, and some remained at release sites for up to 11 months. Some juvenile galaxiids also respond positively to specific concentrations of adult pheromones released into the water by fish in established populations (Baker & Hicks 2003), and are thought to attract juvenile fish to suitable adult habitat. Thus, where desired species are absent or population numbers are very low, active reintroductions of fish to physically suitable sites may be needed to ensure new recruits are attracted to restored streams so that the long-term sustainability of populations can be maintained.

Conclusions

This study illustrates that some urban streams and seepages can provide important habitat for a range of native fish and invertebrate species in city environments, and underscores the importance of identifying and protecting existing ecological values to avoid degradation from future development. The potential for rejuvenation of macroinvertebrate communities appears to be constrained at highly developed sites due to factors primarily associated with stormwater inputs. However, riparian vegetation may help enhance community structure along with biogeochemical function in some streams draining less intensively urbanised catchments. Due to the varied range of local and downstream factors (e.g. passage for migrating species) that can influence native fish community composition, restoration goals for fish in urban streams may be best focused on certain flagship species (e.g. giant kōkopu) and key constraints to long-term population viability (e.g. barriers to migration). While this may not constitute 'restoration' in the literal sense of returning a stream and its biotic assemblages to a previous condition, it would nevertheless make an important contribution to urban biodiversity and conservation of threatened species. Actions potentially contributing to urban stream restoration goals include (1) an integrated catchment approach to resolving passage issues, (2) planting of riparian areas with tree species that provide overhanging vegetation and improved bank stability, (3) active reintroduction of wood to streams to enhance cover and habitat heterogeneity, and (4) seeding of depauperate streams with native fish to help initiate natural recolonisation.

Acknowledgements

We thank Myles Hill and Steve Moore for assistance with collecting and identifying invertebrates, Alex Ring, Dudley Bell, Mike Lake, Bruno David and Warrick Powrie for helping with fish collection, and Bryan Clements for producing the map. Brenda Aldridge's Master of Science studies were funded by a Te Tipu Putaiao fellowship

(UOWX0603) from the Foundation for Research, Science and Technology (FRST), and by Environment Waikato. Funding from Environment Waikato, Hamilton City Council, and other FRST grants to the University of Waikato (UOWX0501) and NIWA (C01X0305) also contributed to aspects of the work. Comments on the manuscript by John Maxted, John Quinn, Mike Winterbourn, Anne Austin and two anonymous referees are appreciated. The work described in this study was carried out under MAF permits SP386 and SP394, and The University of Waikato Animal Ethics Committee protocol no. 675.

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Editorial Board member: Mike Winterbourn

Received 1 December 2008; accepted 26 March 2009

Sire code	Easting	Northing	Fishing method	Invertebrates	SEV
Urban					
B1	2710500	6380300	M	+	+
B2	2710467	6379571	M, S	+	+
F1	2709972	6378958	M, S	+	+
G1*	2711696	6376986	M	+	+
G2	2712102	6377333	M, E, S	+	+
H1	2711426	6375305	M	+	+
K1	2709514	6381687	M, F	+	+
K10	2710753	6382107	M, E, S	+	+
K11	2710700	6381700		+	+
K2*	2710250	6381720	M, S	+	+
K3	2711226	6381356	M, F	+	+
K4	2711223	6381362	M, F	+	+
K6a	2711108	6383218	M	+	+
K8	2710288	6381903	M, F	+	+
K9	2710246	6381922	M, E	+	+
M1	2712751	6374066	M, E, S	+	+
M11	2712228	6374204		+	+
M12	2711453	6374244		+	+
M2	2712231	6373913	M, F	+	+
M3	2712235	6373926	M, F	+	+
M4	2712236	6374178	M, E, S	+	+
M5*	2712550	6374441	M, E	+	+
M6	2712640	6373733	M, E, S	+	+
M7	2712184	6372905	M, S	+	+
N1	2714653	6376777		+	+
S3	2708605	6383764	M, S	+	+
W1	2710146	6378492	M	+	+
W2	2708124	6377130	M	+	+
Seep9	2712575	6373665		A	
Seep8	2712000	6374070		A	
Seep7	2712195	6372955		A	
Seep6	2708445	6377795		A	
Seep5	2709616	6378115		A	
Seep4	2709955	6378520		A	
Seep3	2710730	6382208		A	
Seep2	2710781	6382111		A	
Seep1	2710666	6382008		A	
Periurban					
K5*	2712315	6381065	M, E, S	+	+
K6b	2711106	6383232	M		
M10	2710928	6372869	M, F	+	
M8	2713210	6373473	M, F, E, S	+	+
M9	2712223	6372022	M	+	
Mn1	2715690	6375746	M, F		
Mn2	2715741	6375765	M, F		
Mn3	2715690	6375739	M, E, S		
R1	2705995	6386435		+	+
R2	2705016	6387727		+	+
S1*	2706727	6384425	M	+	
S2	2708416	6383454	M, F	+	+
T1	2706427	6379403	M		
T3	2702543	6381305	M, F		
T4	2702065	6382426	M		
T5	2704524	6380532	M, F		
T6	2704741	6382341	M		
T7	2705533	6383325	M		
T8	2704351	6386562	M		

Appendix 1. Locations and types of samples collected at Hamilton urban and periurban sites. * fish and invertebrate sampling sites more than 100 m apart. M, minnow trapping; S, spotlighting; E, electric fishing; F, fyke netting; + invertebrates and habitat assessed or SEV (Stream Ecosystem Valuation) conducted; A, adult insect sampling.

Appendix 7: 'Early view' reprint of co-authored paper published in River Research and Applications.

Schwendel, A. C., R. G. Death, I. C. Fuller, and J. D. Tonkin. In press. A new approach to assess bed stability relevant for invertebrate communities in upland streams. River Research and Applications.

RIVER RESEARCH AND APPLICATIONS
River Res. Applic. (2011)
Published online in Wiley Online Library
(wileyonlinelibrary.com) DOI: 10.1002/rra.1570

A NEW APPROACH TO ASSESS BED STABILITY RELEVANT FOR INVERTEBRATE COMMUNITIES IN UPLAND STREAMS

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ABSTRACT

Composition and structure of lotic ecosystems can be affected by substrate instability. Consequently stream ecologists have used various methods to determine bed stability characteristics. However, the link between community composition and these measurements varies because benthic biota often responds to combinations of bed stability characteristics. This paper presents a protocol to determine reach-scale stream bed stability in mountain streams which is relevant for invertebrate communities (Stream Bed Stability for Invertebrates, SBSI). The approach is calibrated on community composition response to bed stability but does not measure any single bed stability characteristic *per se*. It consists of 13 parameters that are assessed once at each reach with minimal instrumentation and low interference with the substrate. These 13 parameters cover aspects of sediment supply from banks, transport capacity and substrate erodibility as well as effects of particle transport on channel bottom structures, substrate assemblage and single grains. Application of the SBSI protocol improved the relationship between bed stability and community diversity compared to when conventional bed stability measures were employed. The SBSI protocol provides a cost-effective and time-effective assessment method for bed stability and its application can facilitate research on invertebrate community response to physical disturbance. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS: bedload transport; lotic ecosystem; mountain stream; stream ecology; substrate stability; tracer stone

Received 15 June 2010; Revised 10 June 2011; Accepted 20 June 2011

INTRODUCTION

Flow influences many important structural attributes of stream ecosystems such as substrate stability, habitat volume and channel morphology (Poff and Ward, 1989). Variation in discharge is recognized as one of the fundamental determinants of structure and function of benthic communities in lotic ecosystems (Resh *et al.*, 1988; Reice *et al.*, 1990; Lake, 2000; Death, 2008). Floods can cause movement of coarse bed substrate which can affect the composition of periphyton (Biggs *et al.*, 1999), invertebrate (Cobb *et al.*, 1992; Death and Winterbourn, 1995; Holomuzki and Biggs, 2000), bryophyte (Suren and Duncan, 1999) and macrophyte communities (Riis *et al.*, 2008). However, different groups of biota respond to different aspects of bed stability on a range of scales. For instance, the reaction to patchy scour or fill varied between invertebrate taxa although on a larger scale stable patches might mitigate the effects of substrate instability (Matthaei and

Townsend, 2000). Bed stability is a characteristic feature of alluvial channels comprising aspects like entrainment, transport and deposition of substrate as well as abrasion by suspended material on scales ranging from a single particle to an entire reach. These bed stability characteristics might affect sessile organisms in different ways than more mobile groups of biota (Downes, 1990; Englund, 1991; Holomuzki and Biggs, 2000; McAuliffe, 1984). Consequently, some methods to quantify bed stability perform well with one group of organisms but show only a weak connection with other groups (Duncan *et al.*, 1999; Schwendel *et al.*, 2011a). This in turn is reflected in the wide variety of bed stability measurements used by stream ecologists to examine the effects of flow disturbance (Schwendel *et al.*, 2010).

The effects of substrate movement on stream invertebrate communities via habitat alteration, displacement and death of individuals and changes in their food sources are widely recognized (e.g. Townsend *et al.*, 1997; Matthaei and Townsend, 2000; Effenberger *et al.*, 2006; Death, 2008; Schwendel *et al.*, 2011b). Different levels of bed stability, for example, apparent in depth and pattern of disturbance or in transport distance of particles, are reflected in invertebrate community composition for instance via recolonization abilities of individual taxa (Death, 2008). The methods employed to assess bed stability in relation to

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invertebrate community metrics are reviewed in Schwendel *et al.* (2010) and include calculation of critical shear stress (Newbury, 1984; Cobb *et al.*, 1992; Death and Winterbourn, 1995), FST-hemispheres (Dittrich and Schmedtje, 1995; Merigoux and Doledec, 2004), scour chains (Palmer *et al.*, 1992; Matthaei and Townsend, 2000; Effenberger *et al.*, 2006), scour plates (Palmer *et al.*, 1992), tracer stones (Death and Winterbourn, 1994; Townsend *et al.*, 1997; Death and Zimmermann, 2005; Barquin and Death, 2006), morphological budgeting (Schwendel *et al.*, 2011a) and the Pfankuch Stability Index (Pfankuch, 1975; Death and Winterbourn, 1995; Townsend *et al.*, 1997; Death, 2002). Each of these methods can only assess a distinct set of bed stability characteristics and the strength of the relationship between invertebrate diversity and community composition varies (Schwendel *et al.*, 2011a). The need of site specific calibration (e.g. bedload transport formulae and acoustics sensors) and interference with the substrate (e.g. scour plates and bedload traps) can constrain application for multi site studies and concomitant invertebrate sampling respectively (Schwendel *et al.*, 2010). Insufficient spatial (e.g. bedload samplers) or temporal coverage (e.g. FST-hemispheres) for reach-wide, long-term bed stability assessment can be an additional problem. Further, time and cost constraints can often prevent application of elaborate methods. Visual surveys of stream bed properties such as the Pfankuch Stability Index can circumvent some of these limitations but they can potentially be biased by observers or regional factors such as substrate lithology.

Thus a technique that combines the strengths of elaborate bed stability measurements with the easy application of a visual approach would facilitate research on stream invertebrates and increase comparability between studies. Consequently, this paper presents a straightforward survey protocol specifically calibrated for the assessment of reach-scale stream bed stability relevant for invertebrate community composition (SBSI). It needs to be pointed out that the SBSI survey does not measure any single aspect of bed stability *per se* but determines a characteristic response of invertebrate community composition to a combination of bed stability characteristics. The SBSI was validated at independent sites using *in situ* marked tracer stones and the bottom component of the Pfankuch Index, two techniques that were shown to be well related to invertebrate community metrics (Schwendel *et al.*, 2011a). Additionally the connection between bed stability measured with SBSI and community metrics was explored.

Application for the SBSI method may include scientific studies of disturbance–diversity relationships and habitat characteristics as well as assessment of the potentially confounding effects of bed instability on invertebrate community composition when the latter is employed to determine water quality or environmental status of a stream.

METHODS

Study sites

Data for calibration and validation of SBSI protocol were collected between October 2007 and March 2010 from 54 mountain stream reaches in the southern part of the North Island of New Zealand. They were located in the axial Tararua ($n=12$) and Ruahine Ranges ($n=11$), the Central Volcanic Plateau ($n=13$) and around Mount Egmont ($n=18$) (Figure 1). The former ranges consist of uplifted folded and faulted Mesozoic greywacke and argillite whereas the other mountains are composed of Quaternary andesitic volcanic deposits. Catchment vegetation was dominated by native broadleaf–podocarp forests, scrub and tussock grassland and anthropogenic influence is relatively small (e.g. <0.1% urban land use, 0–45% non-intensive pasture and no infrastructure upstream of sites). Consequently, water quality was expected to be relatively unimpaired. The studied stream reaches varied considerably in substrate assemblage, width, channel form (Table I) and sediment supply (Schwendel and Fuller, *in press*). Substrate composition ranged between gravels and cobbles although some sites contained a considerable proportion of boulders. Riparian vegetation was variable with native forest, willows and poplars, native scrub, non-intensive pasture, tussock and bare ground present. Some of the reaches were laterally confined by vegetated banks, whereas others migrated within a wide active channel zone.

Invertebrate communities

Five Surber samples (500 μm mesh, 0.1 m^2) were collected from riffles during periods of baseflow at least two weeks after the last spate to ensure a characteristic species assemblage was collected. Seasonal variability in New Zealand stream invertebrate communities is generally low (Townsend, 1981; Winterbourn, 2000) however, this was tested and confirmed at 18 of the sites where samples were taken three times throughout the year (Schwendel *et al.*, 2011a and J. Tonkin, unpublished data). Samples were stored in 4% formalin or >60% isopropyl alcohol and later sorted. Very abundant taxa (>300 individuals per sample) were subsampled following Vinson and Hawkins (1996): samples expected to contain large numbers were divided in equal subsamples of which one was initially searched for invertebrates. Only those taxa with number of individuals that did not exceed 300 in the first subsample were searched for in the second subsample. Invertebrates were identified to the lowest possible taxonomic level using the keys in McFarlane (1951), Winterbourn (1973), Townsend and Peters (1996) and Winterbourn *et al.* (2006). Invertebrates were sampled where applicable from riffles because their community composition is likely to reflect gradations in substrate

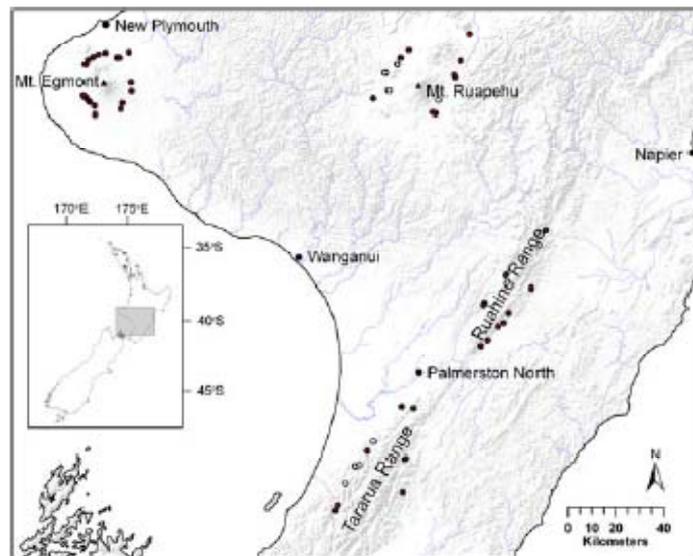


Figure 1. Stream reaches in the southern North Island of New Zealand studied for calibration of the Stream Bed Stability for Invertebrates protocol. Open circles denote the sites used for validation.

stability and, on a larger scale, instability in riffles affects also pools, e.g. via bedload transport.

Periphyton and habitat parameters

At each invertebrate sampling point depth, wetted stream width and near-bottom flow velocity were measured. The latter was recorded over 60 s with an electromagnetic flow meter (Model 801, Valeport Ltd., Tones, UK) 0.05 m above the stream bed. At each site pH and temperature corrected conductivity were measured using Eutech pHestr2 and ECScan Low+ (Eutech Instruments, Singapore) respectively. Percentage aerial cover of riparian land use categories (native vegetation, pasture and willows) within a strip of approximately 5 m and the fraction of dry active channel bare of vegetation under base flow conditions were estimated visually.

Chlorophyll *a* pigment concentration on five gravel-sized stones that were collected beside invertebrate samples was assessed as a measure of periphyton biomass. The stones were transported in the dark in cooled stream water before storing them at -18°C . Pigments were extracted in 90% acetone for 18 h at 5°C in the dark before the chlorophyll *a* absorption was measured using a Cary 50 Conc UV-Visible spectrometer (Varian, Mulgrave, Australia). Chlorophyll *a* pigment concentration was calculated (Steinman and Lamberti, 1996; APHA, 1998) and corrected for stone surface area, which was estimated based on measurement of the *a*-axis,

b-axis and *c*-axis of the gravels with a sliding calliper following Graham *et al.* (1988).

Substrate composition of riffles was assessed by measuring the *b*-axis of >100 randomly collected particles (Wolman, 1954) and classifying them according to a modified Wentworth scale.

Bed stability

Substrate stability was assessed with two established reference measures: tracer particles and the Pfankuch Stability Index. For the development of the new approach, a set of 38 candidate variables (Table II) were selected from a large array of parameters potentially related to stream bed stability (Knighton, 2008; Petts and Foster, 1985) in respect to importance and practicability of assessment with minimal instrumentation in the field. These candidate variables were evaluated at stream sections with a length of approximately five to seven times stream width to include, where present, at least one riffle–pool unit (Keller and Melhorn, 1978).

Candidate variables are associated with the riparian environment (denoted A), the cross (B) and longitudinal profile (C) of the channel, the channel bottom structure (D) and the substrate (E). The density and composition of the riparian vegetation within a 5-m strip along the active channel zone (A1, A3) reflects bank stabilisation by roots, pressure from land use and frequency and magnitude of flood disturbance. Together with bank erosion (B2) and deposition

Table I. Abiotic characteristics of the study sites assessed between October 2007 and March 2010

Site	Stream order (Strahler, 1952)	Mean depth (m)	Mean width (m)	Mean flow velocity (ms ⁻¹)	Mean conductivity ($\mu\text{S cm}^{-1}$)	Mean temperature (°C)	Mean pH	Substrate D ₉₀ (mm)	TTM
Tairarua Range									
Waiohau	4	0.20	6.8	No data	84	11.5	7.5	86	39.94
Waioanuru	5	0.26	17.4	0.716	68	11.3	7.7	84	38.57
Waikawa	4	0.18	6.1	No data	76	13.2	7.5	99	36.78
Panarewae	3	0.11	7.0	No data	74	13.1	7.6	103	31.21
Kiriwhakapapa	3	0.15	6.5	0.603	64	9.7	7.2	59	20.43
Ohau	4	0.24	14.0	0.694	72	12.7	7.6	64	14.30
Pukeatua	3	0.18	9.7	0.720	80	12.4	7.7	84	12.50
Makakaha	4	0.17	6.3	No data	66	19.4	7.4	82	11.18
Manganainoka	4	0.17	11.7	0.694	52	13.3	7.1	108	7.67
Rawnsley	2	0.11	5.1	0.422	48	13.5	6.9	159	4.74
Tokomaru	4	0.14	14.6	0.707	81	17.5	6.9	85	3.07
Kahuterawa	4	0.15	3.5	0.616	68	14.1	6.5	85	0.06
Ruahine Range									
Waipawa	3	0.20	5.4	1.000	103	8.8	8.2	59	79.56
Tamaki	2	0.17	3.3	0.811	64	10.8	7.6	35	64.46
Mangapuaka	2	0.09	2.3	0.584	69	8.6	6.7	28	21.51
Konewa	3	0.10	6.5	0.575	133	13.0	7.5	72	15.36
Rokaiwhana	3	0.22	3.1	0.887	66	14.7	7.1	58	14.96
Makawakawa	4	0.21	27.6	0.630	58	14.3	7.0	83	12.03
Raparaipawai	3	0.17	7.0	0.931	72	13.3	7.3	84	8.44
Makiekie	2	0.19	5.7	0.646	51	10.9	7.3	109	4.86
Coppermine	3	0.13	4.4	0.592	90	13.5	7.4	51	4.43
Manawatu	3	0.20	4.3	0.603	66	9.4	7.8	65	3.85
Cone	2	0.16	4.5	0.588	50	11.0	7.2	107	0.53
Central Plateau									
Mangatotoenui	4	0.26	8.6	0.597	139	7.1	8.0	97	18.70
Waikato	3	0.14	3.2	No data	66	10.0	7.8	18	11.38
Te Piripiri	3	0.19	2.0	0.742	69	8.5	7.7	35	2.09
Wahianoa	3	0.26	6.3	0.967	70	12.8	7.4	145	1.73
Whakapapaui	4	0.28	15.8	0.976	138	11.8	8.2	125	1.02
Oturere	4	0.42	9.4	0.859	112	10.2	8.6	131	0.59
Makomiko	3	0.13	5.3	no data	27	11.3	7.5	107	0.07
Makotuku	2	0.13	5.7	no data	30	9.2	7.4	116	0.03
Waikareke	3	0.23	3.5	0.965	159	10.7	8.1	104	0.01
Mangahua	2	0.20	8.6	no data	38	9.9	7.1	147	0.01
Poua	5	0.44	7.7	1.053	71	10.6	8.0	80	0.00
Oratoha	3	0.24	2.5	0.548	128	12.8	8.3	166	0.00
Pukeonake	4	0.17	6.8	0.398	23	8.2	7.0	158	0.00
Mount Egmont									
Waiahakaho	3	0.25	13.8	0.614	109	16.6	7.9	100	50.00
Timaru	2	0.12	3.6	0.295	69	14.6	6.9	213	34.04
Kaiapahi	3	0.17	11.8	0.756	159	17.5	7.9	172	26.68
Manganui	2	0.15	14.7	1.022	56	18.9	6.7	142	20.77

(Continues)

Table I. (Continued)

Site	Stream order (Strahler, 1952)	Mean depth (m)	Mean width (m)	Mean flow velocity (ms ⁻¹)	Mean conductivity (µScm ⁻¹)	Mean temperature (°C)	Mean pH	Substrate D ₉₀ (mm)	TTM
Waiouana	2	0.13	8.9	0.684	112	15.6	7.7	164	17.74
Kapuni	3	0.14	10.7	0.649	61	14.2	7.2	82	14.46
Paneshu	4	0.21	4.9	0.706	98	13.4	7.7	77	11.91
Mangorei	2	0.12	6.2	0.715	82	15.2	7.3	>300	10.07
Kotikara	2	0.11	2.6	0.403	55	15.5	6.8	168	8.81
Waiuaa	3	0.16	6.7	0.727	130	11.9	7.7	50	8.36
Oakura	3	0.14	7.8	0.412	77	14.0	7.2	239	3.14
Kiri	3	0.17	7.9	0.647	51	17.0	7.2	159	2.60
Waiuaa Forks	3	0.14	6.5	0.890	124	10.7	7.7	146	1.63
Kaupokomui	3	0.18	7.4	0.580	79	18.1	7.5	150	1.56
Oaonui	2	0.12	5.1	0.796	102	13.7	8.0	73	1.06
Cold	1	0.21	3.4	0.797	80	10.0	7.3	74	0.98
Patea	3	0.21	8.4	0.486	72	12.3	7.0	192	0.31
Waiuaa trib.	3	0.19	4.3	0.751	113	11.0	7.5	133	0.02

Depth, width, velocity, conductivity, temperature and pH measurements are averaged from five readings taken concomitant with invertebrate sampling. TTM is an index of bed stability calculated from the movement of *in situ* marked tracer stones. Sites used for validation are in italics.

of derived fine sediments (B3), these parameters indicate sediment supply from banks and slopes. These processes influence substrate characteristics (E3–6), which can be relevant for bed stability. Transport capacity is assessed in terms of available potential energy (slope) (C1), expenditure on roughness elements (D6), channel adjustments (C2, D4) and flood regime (A2). The channel dynamics resulting from sediment supply and transport capacity are reflected in channel form (B1), structures (D1, D3–5), aquatic vegetation (D2) and substrate characteristics (E1–4, E7). Additionally, lithology of the substrate, weather (sunny, overcast or rain) and state of the floodplain substrate (dry or wet) were recorded because these factors could potentially interfere with visual evaluation methods such as the Pfankuch Index (A. C. Schwendel, unpublished data).

Tracer particles were used to assess stream bed stability. Five randomly selected tracer stones in each of three size classes (D₅₀, D₇₀ and D₉₀) were marked with radio-frequency identification tags (23mm glass tags, Texas Instruments, Dallas, USA), which were attached *in situ* to stones in riffles using wet curing epoxy-concrete (K273, Nuplex Construction Products, Hamilton, New Zealand). When high turbulence or fast flow velocity prevented underwater application (11% of particles), stones were removed from the river bed for tag attachment and afterwards carefully re-embedded. The percentage of entrained *in situ* marked tracer stones and re-embedded tracers was significantly correlated (Spearman rank correlation, $R=0.70$, $d.f.=26$, $p=0.0001$). Relocation and identification of each tracer stone was carried out contactless using a portable antenna and datalogger (OregonRFID, Portland, USA). Initial and subsequent positions of tagged stones were surveyed using high precision differential GPS or were marked on riparian vegetation and stable banks. Relocation surveys took place approximately every two months or after high-discharge events over a total period of six months. The entire bed and active channel downstream of the last position of each tracer particle were searched intensively to the next local sediment trap (e.g. riffle) beyond a minimal distance of 50m. Stones that could not be recovered were assigned a travel distance of 50m. Although this was less than usually searched, it accounted for tracers lost by deep burial (>0.6m), storage in inactive parts of the floodplain, tag damage and malfunction. The travelled distance of the tracer particles was converted to an index of bed stability (TTM=sum of tracer movement) using the following approach:

$$TTM = (d_{50} * s_{50}/n_{50} + d_{70} * s_{70}/n_{70} + d_{90} * s_{90}/n_{90}) / (d_{50} + d_{70} + d_{90}) \tag{1}$$

The sum of the moved distance *s* of stones of a size class between the surveys is divided by the counted recoveries *n*

Table II. Assessed properties of the channel, banks and riparian environment potentially related to bed stability

Variable	Description
Riparian environment	
A11	Fraction of pasture on riparian strip (%)
A12	Fraction of native forest on riparian strip (%)
A13	Fraction of exotic vegetation on riparian strip (%)
A14	Fraction of scrub on riparian strip (%)
A15	Fraction of other land cover (none, tussock, etc.) on riparian strip (%)
A21	Ratio of floodplain width to active channel width (m/m)
A22*	Ratio of floodplain width to wet channel width (m/m)
A23	Ratio of active channel width to wet channel width (m/m)
A31	Percentage of high bank surface covered with vegetation (%)
A32	Variation in species and age of high bank vegetation (categorical)
Channel cross profile	
B11	Channel incision, ratio of width to depth (m/m)
B21	Bank erosion (categorical)
B22	Number of recent bank collapses
B31	Number of recently deposited lateral bars of fine material (< coarse gravel)
Channel longitudinal profile	
C11	Bed slope (m/m)
C21	Sinuosity (categorical)
Channel bottom	
D11	Fraction of area affected by erosion and deposition (%)
D21	Occurrence and form of aquatic vegetation (categorical)
D31	Number of multiple barforms
D32	Fraction of area occupied by multiple barforms (%)
D41	Number of riffle-pool and step-pool sequences
D51	Occurrence of bedform clusters (categorical)
D61	Fraction of area with supercritical flow (%)
Substrate	
E11	Grain angularity (categorical)
E21	Constitution of grain surface (categorical)
E31	Interlock and overlap between particles (categorical)
E41	Packing and compaction of particles (categorical)
E51	Fraction of sand and smaller grain size (% area)
E52	Fraction of gravels (% area)
E53	Fraction of cobbles (% area)
E54	Fraction of boulders (% area)
E55	Homogeneity (% area of most abundant size class/ number of size classes present)
E56*	Size index (Sum of fractions weighted by their geometrical mean size of their size class)
E57*	Mean size index (Size index/ number of size classes present)
E58*	Fraction of cobbles and gravels (% area)
E61	Fraction of stable material (large boulders and bedrock) (%)
E71	Occurrence of an armour layer (categorical)

Categorical variables were rated at a scale from 1 (associated with stable substrate) to 4 (associated with substrate instability), * variable removed because of intercorrelation.

and weighted by the geometric mean particle size d of that class.

As a second independent measure of bed stability, the bottom component of the Pfankuch Stability Index

(BCP) (Pfankuch, 1975) was employed once at each site. The bottom component was preferred over the total index because in previous studies it showed a better relationship with other measures of bed stability (Death and Winterbourn, 1994) and is well related to biological data (Death and Winterbourn, 1995; Suren, 1996). It involves allocation of an observer's subjective visual evaluation of six attributes, including substrate brightness, angularity, consolidation of particles, percentage of stable materials, evidence of scouring and state of clinging aquatic vegetation, to four predetermined categories to which scores are weighted according to their perceived importance. The sum of the scores results in a stability index, where high values represent low stability.

Data analysis

The collected data were examined in four steps: (i) analysis of invertebrate community composition and structure; (ii) development of the SBSI protocol; (iii) exploration of the relationship between SBSI, other measures of bed stability and community metrics; and (iv) validation of the SBSI protocol at independent sites in respect to other bed stability measures and relevance for invertebrate communities.

The composition of the invertebrate community at 46 calibration sites (Figure 1) was explored with non-metric multidimensional scaling (NMDS) in PC-ORD 5.0 (MjM Software, Gleneden Beach, USA) using standardised (by maximum) invertebrate taxa abundance. Association of the derived axis scores with measured environmental parameters and selected variables from the Freshwater Environments of New Zealand database (Wild *et al.*, 2005) was assessed using Pearson's correlation. The axis that was best correlated to conventional bed stability measures, TTM and BCP, was selected for calibration of the SBSI. Community diversity (Brillouin Index), taxa number, rarefied taxa number (for 200 individuals following Sanders (1968) and Hurlbert (1971)) and mean number of individuals per 0.1 m² were calculated for all sites in PRIMER v6 (Plymouth Marine Laboratory, Plymouth, UK).

The SBSI was developed with linear best subset regression (Statistix 9.0, Analytical Software, Tallahassee, USA) using the selected NMDS axis as dependent variable and the 38 parameters assessed in the field (Table II) as independent variables. Adjusted R², residual mean square error, Mallows' Cp, predicted residual sum of squares and Akaike's Information Criterion for small samples were used to compare models.

The relationship between the SBSI site scores, bed stability measured with tracer stones and the bottom component of the Pfankuch Index and invertebrate community metrics was assessed with Spearman rank correlation to account

for the non-normal distribution of variables. This was accomplished for the 46 sites used for SBSI calibration to show the relevance of the SBSI for invertebrate communities and separately for the eight validation sites. The latter consisted of four randomly selected reaches in each of the two bedrock regions (volcanic and sedimentary) in order to account for variations in shape and colour of the substrate. Significance from the multiple correlations was adjusted using false discovery rate correction (Benjamini and Hochberg, 1995).

RESULTS

Invertebrate community

A total of 127 invertebrate taxa were collected across the 46 SBSI calibration sites with a mean number of individuals per 0.1m² of 194 consisting of on average 33 taxa. Overall Trichoptera comprised the largest number of taxa (35%), followed by Diptera (25%) but the samples were numerically dominated by Ephemeroptera larvae (45% of individuals) of which *Deleatidium* was most common (100% of sites) and abundant (42% of individuals).

Ordination (2D stress 0.16) revealed that only one axis was strongly correlated with bed stability measured with tracer stones and the bottom component of the Pfrankuch Index (Table III). This axis was also associated with periphyton biomass and the fraction of the active channel bare of vegetation (Figure 2). It was subsequently used to calibrate the SBSI. Sites associated with low bed stability were found in the Ruahine Ranges and around Mount Egmont and were dominated by *Deleatidium*. In contrast, very stable sites were located mostly on the Central Plateau and had a richer fauna and higher number of individuals.

Stream Bed Stability for Invertebrates protocol

Any intercorrelated variables of assessed reach properties were removed from further analysis (Table II). Weather and substrate surface wetness were not significantly correlated with other variables but substrate lithology (andesite and greywacke) was significantly correlated to grain angularity (E11) (Spearman's *R* 0.82, d.f. =45, *p*=0.0001). Andesitic stones were more rounded than greywacke clasts prior to fluvial transport. Consequently scores for grain angularity were raised by one class at sites with greywacke-dominated substrate. Best subset regression, using the NMDS axis best correlated to bed stability measures as dependent variable and the refined set of reach properties as independent variables, led to the identification of an optimal model (Table IV). This model of stream bed stability relevant for invertebrates (SBSI) comprises 13 variables, which reflect mostly direct effects of channel dynamics observed on the banks

Table III. Correlation of bed stability measurements (total tracer movement—TTM, bottom component Pfrankuch Index—BCP), measured (marked with *) environmental parameters and periphyton biomass and downstream variables, segment variables and runoff-weighted upstream catchment variables from the Freshwater Environments of New Zealand database (Wild *et al.*, 2005) with non-metric multidimensional scaling axes

Axis	Pearson's <i>R</i>	
	1	2
Width*	-0.06	0.06
Depth*	0.33	-0.20
Velocity*	0.12	-0.19
Conductivity*	0.22	-0.03
Temperature*	-0.17	0.13
pH*	0.33	-0.09
Riparian pasture*	0.18	0.25
Riparian bare floodplain*	-0.44	-0.33
Periphyton biomass*	0.44	0.13
Average slope of downstream network	-0.31	0.09
Maximum slope of downstream segments	0.18	-0.10
Maximum segment slope based on 30m grid	0.03	0.17
Segment sinuosity	-0.05	0.07
Average segment slope	-0.26	-0.12
Shaded fraction of segment	-0.02	0.06
Percentage of the segment riparian area covered in scrub	0.20	0.13
Upstream mean January air temperature	0.06	0.49
Upstream catchment rain days > 15mm/month	-0.27	0.13
Upstream lake index	0.19	0.00
Percentage of upstream catchment annual runoff from alluvium	0.12	0.13
Percentage of upstream catchment annual runoff from peat	-0.12	-0.03
Upstream average of calciferous regolith	-0.19	0.14
Upstream catchment average of regolith hardness	-0.10	-0.06
Upstream catchment average of particle size	-0.05	0.04
Percentage of upstream catchment consists of bare ground	0.15	-0.62
Percentage of upstream catchment covered in exotic forest	0.25	-0.10
Percentage of upstream catchment covered in indigenous forest	-0.08	0.39
Percentage of upstream catchment with pastoral land use	0.17	0.09
Percentage of upstream catchment covered in tussock	-0.04	-0.25
Percentage of upstream catchment consist of wetland	0.10	0.10
Segment stream order	0.18	-0.02
TTM	-0.53	0.04
BCP	-0.57	0.09

Significant correlations are marked bold (*p*<0.01).

and at the channel bottom. Sediment supply and transport capacity are represented with two variables each, which are assessed on the banks and the longitudinal channel

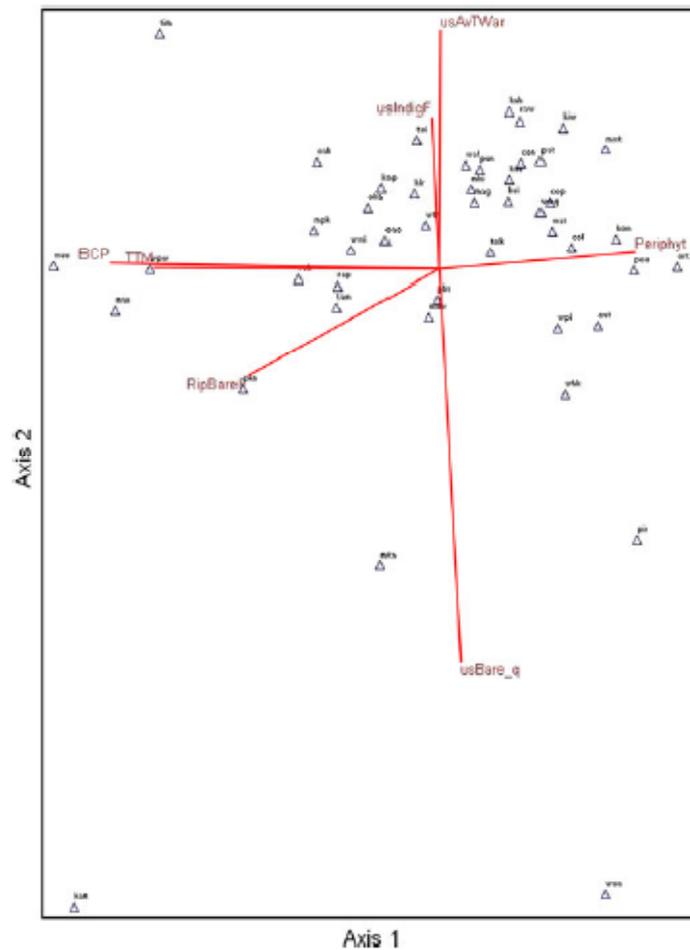


Figure 2. Non-metric multidimensional scaling axes of 46 mountain stream invertebrate communities and correlated parameters ($p < 0.01$). Periphyt, periphyton biomass; usAveTWar, Upstream mean January air temperature; usIndigF, Percentage of upstream catchment covered in indigenous forest; TTM, total tracer movement; BCP, bottom component of Pfankuch Index; RipBareF, Dry active channel bare of vegetation under base flow condition; usBare_q, Percentage of upstream catchment consisting of bare ground.

profile. Substrate parameters (size and compaction) constitute a second group mirroring the effects of sediment dynamics such as sorting. Low variance inflation factors (VIP) indicated that collinearity between the variables is low.

On the basis of the regression model, a field sheet (Appendix 1) was designed that facilitates recording of the variables and allows, with the help of a pocket calculator, rapid on-site assessment of bed stability. Channel, bank and substrate properties are to be recorded, noted in relevant fields and multiplied with their respective coefficient. The sum for each compartment (e.g. banks, longitudinal profile, channel bottom and substrate) is recorded on the right hand

side of the sheet and this column is then added up to result in the SBSI site score.

Bed stability and community metrics

Correlation between the SBSI site scores and community diversity (Brillouin Index), taxa number, rarefied taxa number and mean number of individuals was highly significant (Table V). These community metrics were also correlated with bed stability measured with tracers (except taxa number) or the bottom component of the Pfankuch Index but the connection was always weaker than with the SBSI.

Table IV. Results of the regression analysis of the non-metric multidimensional scaling axis against 39 characteristics of the channel and the riparian environment ($R^2=0.805$, adjusted $R^2=0.726$)

Variables	Coefficient	Standard error	t-test if slope $\neq 0$	p value	VIF
Constant	-6.31006	1.00297	-6.29	0	0
A23	0.21652	0.06028	3.59	0.0011	2.1
A31	0.01239	0.00375	3.31	0.0023	1.8
B21	0.26123	0.06495	4.02	0.0003	2
C11	0.05583	0.02096	2.66	0.012	1.3
D11	0.29004	0.09619	3.02	0.005	3.2
D31c	0.28711	0.07222	3.98	0.0004	3
D32	0.012	0.00556	2.16	0.0385	1.9
D51c	0.27049	0.07771	3.48	0.0015	1.6
E11	0.2418	0.12253	1.97	0.0572	1.5
E21	0.16677	0.09457	1.76	0.0874	2.6
E41	0.25041	0.11964	2.09	0.0444	1.7
E51	0.02885	0.00937	3.08	0.0042	2.2
E55	0.0524	0.02019	2.6	0.0141	3.1

VIF, variance inflation factor.

The three measures of bed stability were intercorrelated with the strongest relationship apparent between the bottom component of the Pfankuch Index and SBSI site scores (Table VI).

Validation at independent sites

At eight randomly selected sites a linear relationship was found between bed stability assessed with the bottom component of the Pfankuch Index and the SBSI protocol (Table VI). In contrast, the tracer measure was not correlated with any of the two former; however, correlation coefficients were similar or higher than at the sites used for SBSI calibration and the failure of detection of a significant relationship might be due to the low number of sites. Correlation between the Brillouin Index and SBSI site scores was stronger than with any of the other bed stability measures (Table V). In contrast taxa number, rarefied taxa number and the mean number of individuals were slightly better related to the bottom component of the Pfankuch Index.

Table V. Correlation of invertebrate community metrics with bed stability assessed with the Stream Bed Stability for Invertebrates (SBSI) protocol, *in situ* marked tracer stones (TTM) and the bottom component of the Pfankuch Stability Index (BCP) at 46 New Zealand streams used for SBSI calibration and at 8 independent sites from the same regions for validation

	SBSI calibration sites			Validation sites		
	SBSI	TTM	BCP	SBSI	TTM	BCP
Brillouin Index	-0.75***	-0.52***	-0.68***	-0.81*	-0.78*	-0.73*
Taxa number	-0.56***	-0.27	-0.54***	-0.73*	-0.34	-0.82*
Rarefied taxa number for 200 individuals	-0.77***	-0.51***	-0.55***	-0.73*	-0.40	-0.82*
Mean number of individuals	-0.75***	-0.35*	-0.45**	-0.74*	-0.34	-0.86*

Significance from multiple correlations was adjusted using False Discovery Rate and is indicated by * for $\alpha=0.05$, ** for $\alpha=0.005$ and *** for $\alpha=0.001$.

DISCUSSION

The presented protocol for assessment of bed stability relevant for invertebrates (SBSI) produces site scores highly related to invertebrate community diversity and structure. This connection is stronger than that of any traditional bed stability measure with community metrics at the calibration sites. The SBSI method is calibrated on the response of invertebrate communities, signified by an NMDS axis, to varying degrees of bed stability as measured with traditional techniques and compares well to the NMDS calibration axis (Table VI, Figure 3). The NMDS axis used for calibration of the SBSI is strongly associated with bed stability measures and periphyton biomass. Periphyton as a potential food source for invertebrates influences invertebrate community composition (Death, 2002) but biomass itself is affected by bed movement and can consequently be seen as a proxy for bed stability. The link of the NMDS calibration axis with the percentage of bare active channel reflects the flood regime, which influences bed stability. Lack of vegetation on the banks can indicate regular inundation with flows competent to strip vegetation and to prevent perennial plant growth. Alternatively, it can be caused by active bank erosion during lower discharges when undercutting of banks can lead to failure. This reflects a high degree of channel activity and sediment input and accordingly bed disturbance. Hence it is reasonable to interpret the NMDS axis as being dominated by bed stability.

Validation at independent sites showed the applicability of the SBSI approach and its relevance for invertebrates. Connection with community diversity is improved when the SBSI is used compared with other bed stability measures but the bottom component of the Pfankuch Index performs slightly better with number of taxa and individuals (Figure 4). However, the SBSI approach can account for regional variation in parameters such as lithology and should be less affected by observer subjectivity than the purely visual assessment of the Pfankuch Index.

The parameters of the SBSI model are summarized in Table VII. Theoretically, the total SBSI score ranges between

Table VI. Correlation of bed stability assessed with the Stream Bed Stability for Invertebrates (SBSI) protocol, *in situ* marked tracer stones (TTM) and the bottom component of the Pfankuch Stability Index (BCP) at 46 New Zealand streams used for SBSI calibration and at eight independent sites from the same regions for validation

	SBSI calibration sites		Validation sites	
	TTM	BCP	TTM	BCP
SBSI	0.48***	0.66***	0.47	0.75*
BCP	0.46**		0.67	

Significance from multiple correlations was adjusted using False Discovery Rate and is indicated by * for $\alpha=0.05$, ** for $\alpha=0.005$ and *** for $\alpha=0.001$.

19 (stable) and 201 (unstable) when extreme values for all parameters are assumed. However, the calibration sites, which, according to the bed stability measurements, include both very stable and unstable reaches, cover a range of only 62 to 88. Thus values higher than 80 represent sites with low bed stability, whereas SBSI smaller than 70 indicates high bed stability. The substrate sand fraction and homogeneity are potentially the most powerful parameters but their extreme values seldom occur in mountain streams. At the calibration sites, bank vegetation cover and abundance of multiple barforms had the highest mean scores (10.8 and 9.1 respectively) whereas slope, area of multiple barforms and sand fraction achieved lowest mean scores (<2.3). In the following section, for each parameter, the relation to bed stability is explored, and assessment in the field with the help of the provided field sheet (Appendix 1) is described.

Friction slope determines the total energy available for transport and entrainment of particles in a stream. Water surface or stream bed gradient is often used as a surrogate because it is easier to measure (Schwendel *et al.*, 2010).

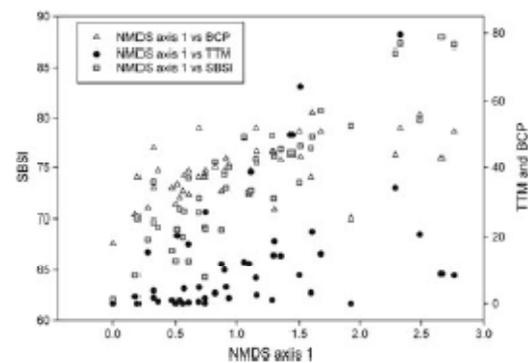


Figure 3. Stream bed stability assessed with the Stream Bed Stability for Invertebrates Index (SBSI), *in situ* marked tracer stones (TTM) and the bottom component of the Pfankuch Stability Index (BCP) plotted against the non-metric multidimensional scaling (NMDS) axis used for calibration of the SBSI.

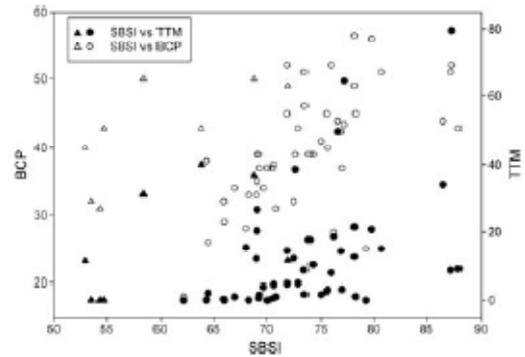


Figure 4. Site scores of the Stream Bed Stability for Invertebrates Index (SBSI) plotted against conventional measures of bed stability: *in situ* marked tracer stones (TTM, closed symbols) and the bottom component of the Pfankuch Stability Index (BCP, open symbols). Sites used for validation are shown as triangles.

When the ratio of flow depth to roughness element height is high (e.g. during high discharge), this is an acceptable first-order approximation. Bed slope can be estimated in the field, if necessary, with the help of an Abney level.

The active channel includes the zone that is dry at baseflow stage but is subject to regular inundation. It is well coupled to the channel and it is involved in processes of sediment transport. In the field, this zone can be determined by the absence or scarcity of perennial vegetation and the presence of recent flood debris. The ratio of the active channel width to wetted

Table VII. Parameters of the Stream Bed Stability for Invertebrates (SBSI) survey with weights and potential range of values (*extreme values estimated) and scores

Parameter	Weight	Range	Minimum score	Maximum score
C11 Bed slope	0.56	0.0001*-1*	0.00006	0.56
A23 Active/wet channel	2.17	1-10*	2.17	21.7
B21 Bank erosion	2.61	1-4	2.61	10.44
A31 Bank vegetation cover	0.12	0-100	0	12
E51 Sand fraction	0.29	0-100	0	29
E55 Substrate homogeneity	0.52	4-100	2.08	52
E41 Packing and compaction	2.50	1-4	2.50	10.0
E21 Particle surface	1.67	1-4	1.67	6.68
E11 Grain angularity	2.42	1-4	2.42	9.68
D11 Reworked area	2.90	1-4	2.90	11.60
D31 Multiple barform number	2.87	0-5	0	14.35
D32 Area of multiple barforms	0.12	0-100	0	12
D51 Bedform clusters	2.70	1-4	2.70	10.80
Total SBSI			19.05	200.81

baseflow channel width is low (e.g. close to 1) for hydrologically stable streams with small variation in flows (e.g. lake fed). With increasing frequency and magnitude of floods, a higher ratio is expected although local geomorphology can interfere (e.g. narrow valleys, bedrock constrictions and bank composition). Both this parameter and stream bed slope quantify potential transport capacity and are expressed on a continuous scale. Considering the potential range of values, bed slope has much less weight than the active channel to baseflow channel width ratio in the regression model.

The sediment supply from banks and lateral channel erosion is represented by the categorical parameter bank erosion. It is evaluated in the field on a scale ranging from none to weak and moderate to strong. Strong bank erosion means that eroded surfaces or collapsed banks are present throughout the reach and that lateral erosion is severe. Moderate bank erosion depicts a state where either light and discontinuous bank erosion is common or locally bank erosion is strong. The category 'weak bank erosion' is chosen when only patchy and light bank erosion occurs. Extrinsic causes for bank collapse such as trampling cattle or human interference are included in this parameter and are not separately assessed.

The percentage of riparian vegetation cover of the upper banks (above bankfull stage) specifies the average vegetation density of the understorey (e.g. stems per m²), not the canopy cover along both sides of the reach. It was expected to be positively related to bed stability because vegetation reduces surface erosion and dense roots stabilise the banks. However, regression showed an inverse relationship to bed stability, which can be explained by land use, altitude aspects and bank composition. The sites with low bank vegetation cover were either in high altitude locations on the Central Volcanic Plateau or natural vegetation was scarce. Anthropogenic land use practices like forestry or gravel mining on floodplains can cause low density of bank vegetation. They are only profitable on relatively stable ground thus reflecting bank stability. Altitude mirrors catchment size and is thus related to stream power. Hence high altitude sites above the tree line with low vegetation cover have usually more stable upper banks than low altitude sites. This parameter combines these two causes of bank vegetation cover, although bank protection by roots is obviously of less importance on the infrequent flood-affected upper banks. We used an accuracy of 5% for bank cover estimations.

Substrate size distribution reflects erosion, sedimentation and transport processes. Fine particles require less shear force for selective entrainment than coarse grains. Hiding and protrusion effects can prevent selective entrainment but visual surface substrate assemblage assessment does usually capture only patches dominated by sand and not hiding sand grains between larger particles. Thus the percentage of sand and smaller grain sizes present and the associated low critical shear stress can indicate high sediment mobility given sufficient

transport capacity. Erosion and sedimentation of sandy substrate and associated changes in habitat can cause shifts in invertebrate community composition (Palmer *et al.*, 1992; Downes *et al.*, 2006).

Substrate size homogeneity can be caused by sorting (e.g. downstream fining) but depends also on catchment substrate lithology and sediment sources (reworking of older alluvial deposits, hillslope collapses or fresh tributary inputs). However, in mountain streams where substrate variety is usually limited by catchment size, sorting can be instrumental for substrate size composition. Because sorting processes require substrate movement, the parameter 'substrate homogeneity' is positively related to instability. In the field it requires estimation of the percentage cover of the size classes such as silt (<0.063 mm), sand (0.063–2 mm), gravel (2–64 mm), cobble (64–256 mm) and boulder (>256 mm). Then the aerial cover fraction of the dominant size class is divided by the number of classes present.

Packing and compaction of particles is highly developed in stable substrate channels. It can be an effect of incompetent flows or lack of sediment supply. This parameter should not be confounded with overlap of particles because of the stone shape of some lithologies. It can easily be tested by walking in the bed and four categories are distinguished. Tight packing means that in the entire channel stones move only minimally when full body weight is applied or the channel bottom consists of bedrock. Wedged packing depicts conditions where only parts of the channel have tight packing or where the entire substrate moves under the foot but does not principally change position (e.g. is entrained afterwards). The 'moderately loose' category includes a mix of all four categories throughout the channel skewed towards looser conditions. Stones may change position when stepped on but should not be entirely dislodged. Loose packing means that the foot sinks into the substrate and particles move easily.

The categorical parameter 'Constitution of particle surface' has been modified from the categories of brightness defined by Pfankuch (1975). It incorporates surface roughness and brightness, which can be effects of particle movement. However, it needs to be distinguished between different lithologies (e.g. limestone and volcanic rocks), which have varying spectra of colours and brightness. Particles of different geological origin can have variable surface roughness after the same transport length. Stains and plant growth on stones are dependent on temperature, light, nutrient levels and mineralization. It is also advisable to allow for weather conditions and surface moisture when stones on the floodplain are investigated: wet surfaces on a rainy day can appear much duller than in dry and sunny conditions. The categories range from more than 95% of stained particles with considerable organic film and growth, over '65–95% dull' and '35–65% dull' to less than 35% dull.

The parameter 'Grain angularity' was also adopted from the Pfankuch Index. It ideally expresses the amount of work

performed on a particle during fluvial transport but the characteristic depends very much on lithology in terms of hardness, cleavability, stratification and mineral content as well as distance from source. Thus adjustment of the scores of sharp and angular rock types such as mudstone and greywacke to the scores of particles that are already rounded prior to fluvial transport (e.g. some volcanic rocks) by the observer is recommended. The categories include particles that are well rounded in all dimensions with smooth surfaces, corners and edges; well rounded in two dimensions, corners and edges; rounded combined with flat surfaces and sharp edges; and corners with roughened surfaces.

The percentage of reworked area describes the amount of obvious recent erosion (e.g. bright sections) and sedimentation (bars of fines, filled pools) of the channel bottom. A fraction of more than 80% is rated as very high, 50–80% as high, 20–49% as intermediate and less than 20% as low.

Multiple barforms are a feature of dynamic channels able to adjust to changing sediment supply and floods. However, over a short term they can be relatively stable channel structures, creating various habitats and providing potential refugia during smaller spates. Surprisingly, the number of multiple barforms is positively related to bed stability in the SBSI model, which might reflect habitat heterogeneity. In contrast their size as a fraction of the total bed area decreases with SBSI bed stability because large areas of multiple barforms indicate substantial channel dynamics. The number of multiple barforms is classified in six categories, which are indexed from zero to five.

Bedform clusters locally influence flow turbulence causing expenditure of energy, which is not available to entrain substrate. They are commonly thought to be resistant to entrainment during high-discharge events (de Jong, 1992; Reid *et al.*, 1992) but depending on flood magnitude, bed form clusters can be as unstable as single surface stones (Matthaei and Huber, 2002). Thus their suitability as refugia for invertebrates and periphyton varies and they do not necessarily support richer invertebrate faunas because of increased habitat heterogeneity (Biggs *et al.*, 1997; Francoeur *et al.*, 1998; Matthaei and Huber, 2002). For the SBSI protocol, abundance of bedform clusters is estimated in the field visually and categorized in four classes ranging from none to abundant (e.g. >5% aerial cover).

CONCLUSIONS

The method presented here for reach-scale assessment of bed stability relevant for invertebrate communities in upland streams seeks to combine statistically derived relationships between bed stability characteristics and the invertebrate community and causal connections. This distinguishes it from other approaches, which aim to measure characteristics of bed stability *per se* but often are not very well related to

responses of different groups of biota. The SBSI protocol provides a similar or stronger connection with community diversity and composition than traditional bed stability measures. Index calibration was conducted in upland streams to avoid the confounding effects of water quality on invertebrate communities but potentially, the SBSI protocol could be applied to a wide range of streams. The SBSI method is straightforward, cost-effective and time-effective and requires minimal instrumentation (Abney level and pocket calculator) and only one site visit is necessary. Interference with the substrate is low, which facilitates concomitant invertebrate sampling and the stability score can be calculated on-site. It should suffer less from difficulties of purely visual assessments (such as the Pfankuch Index) and can account for regional differences (e.g. in lithology). However, observer bias potentially can be a problem. This and applicability at independent sites need to be tested to allow analysis of deficits and adjustments.

ACKNOWLEDGEMENTS

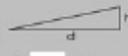
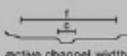
We thank Emslaw One Limited and other land owners for site access. We want to acknowledge two anonymous reviewers for their helpful comments on the manuscript.

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APPENDIX 1

Stream Bed Stability relevant for Invertebrates									
River <input type="text"/>		Date <input type="text"/>		Observer <input type="text"/>					
Reach <input type="text"/>		Coordinates <input type="text"/>		Altitude <input type="text"/>					
Weather: sunny overcast rain		Surface conditions: dry wet		Lithology <input type="text"/>					
Bed slope  h <input type="text"/> m d <input type="text"/> m s = h/d = <input type="text"/>		Floodplain  active channel width f <input type="text"/> m wetted channel width (baseflow) c <input type="text"/> m r = f/c = <input type="text"/>		Bank erosion strong 4 moderate 3 weak 2 none 1 b <input type="text"/>		Bank vegetation cover v = <input type="text"/> %			
s * 0.56 = <input type="text"/>		r * 2.17 = <input type="text"/>		b * 2.61 = <input type="text"/>		v * 0.12 = <input type="text"/>		SUM <input type="text"/>	
Substrate composition s1 silt (<0.063 mm) <input type="text"/> % s2 sand (<2 mm) <input type="text"/> % s3 gravel (2 - 64 mm) <input type="text"/> % s4 cobble (64 - 256 mm) <input type="text"/> % s5 boulder (> 256 mm) <input type="text"/> %		Substrate heterogeneity number of fractions present n <input type="text"/> % of dominant fraction m <input type="text"/> u = m/n = <input type="text"/>		Packing + compaction loose 4 moderately loose 3 wedged 2 tight 1 p <input type="text"/>		Particle surface <35% dull 4 35-65% dull 3 >65% dull 2 dark, stained 1 d <input type="text"/>		Grain angularity edges & corners: a <input type="text"/> well rounded in 3D 4 well rounded in 2D 3 rounded 2 sharp 1	
s2 * 0.29 = <input type="text"/>		u * 0.52 = <input type="text"/>		p * 2.50 = <input type="text"/>		d * 1.67 = <input type="text"/>		a * 2.42 = <input type="text"/>	
SUM <input type="text"/>		SUM <input type="text"/>		SUM <input type="text"/>		SUM <input type="text"/>		SUM <input type="text"/>	
Reworked area e <input type="text"/> >80% 4 60-80% 3 20-49% 2 <20% 1		Multiple barforms number g <input type="text"/> 0 5 1 4 2 3 3 2 4 1 5+ 0		Bedform clusters area k <input type="text"/> % abundant 4 common 3 some 2 none 1 t <input type="text"/>		Channel bottom o <input type="text"/>			
e * 2.90 = <input type="text"/>		g * 2.87 = <input type="text"/>		k * 0.12 = <input type="text"/>		t * 2.70 = <input type="text"/>		SUM <input type="text"/>	
SUM <input type="text"/>		SUM <input type="text"/>		SUM <input type="text"/>		SUM <input type="text"/>		SUM <input type="text"/>	
SBSI <input type="text"/>		SBSI <input type="text"/>		SBSI <input type="text"/>		SBSI <input type="text"/>		SBSI <input type="text"/>	