MASSEY UNIVERSITY
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THE EFFECTS OF HYDROLOGICAL AND NUTRIENT DISTURBANCE ON STREAM INVERTEBRATE COMMUNITIES USING A TRAIT-BASED APPROACH

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Yen Dinh Thi Hai

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Abstract

Anthropogenic altered flow regimes and nutrient enrichment can cause significant impacts on stream biota and may lead to species loss if characteristics of the local fauna are not compatible with the new environmental conditions. I used fourth corner models, Bayesian ordination, and regression analysis to assess those potential effects on trait and species composition of invertebrate communities in UK, New Zealand (NZ) and Vietnamese streams.

NZ temperate mountain streams with greater substrate disturbance increased the abundance of plastron- respirers, but not those having two aquatic life stages or who were filter feeders. UK temperate rivers with predictable multiple high flows per year supported individuals having highly synchronized life history strategy; rivers with one prolonged rising climb and strong groundwater influence were better for those having a high reproduction strategy, and rivers with a steep peak flow supported both strategies.

Nutrients affect functional feeding and life history traits via promoting algal overgrowth in NZ streams. Both periphyton biomass and nutrients increased the abundance of algae piercers, collectors and those having two aquatic life stages, being long-lived and having hermaphroditic ability; but decreased the abundance of shredders, scrapers, and those having univoltine life cycles.

The post-flood recovery of invertebrate communities depended on the recovery of the food base of the food web that was, in turn, determined by the presence of a forest canopy cover and nutrient levels in a stream. Within the forest canopy stream, communities in the low nutrient site recovered by week 9 after a 1-in-50-year flood in Wellington, NZ. Without the forest canopy, the recovery of communities in nutrient-impacted streams (by 25 weeks) was probably associated with a quicker regrowth of periphyton while communities in the low nutrient site had not recovered even after 40 weeks.

Hydrological disturbances, nutrients, and their combination had strong effects on invertebrate communities in temperate streams. Taxa that survive in a site have trait characteristics that are highly compatible with both the hydrological and nutrient conditions at a site. In contrast to temperate invertebrate communities, Vietnamese tropical highland community structure was influenced more by elevation than disturbance. Further studies are required to clarify how flow disturbance may effect invertebrate communities in tropical streams.

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Preface

The thesis was written up in the format of a paper-based thesis, therefore, each chapter was presented as a standalone manuscript. Consequently, information in methodology in each chapter may be repeated. Chapter 1-8 are primarily my work with input from my chief supervisor, Professor Russell Death.

Professor Russell Death provides critical contribution on manuscript development and editing. Therefore, he is a co-author on all manuscripts prepared. Wendy Monk and Paul Wood are co-authors on Chapter Two because they supplied the hydrological and raw invertebrate data for analysis. Hieu Quang Nguyen is a co-author on Chapter Five because he identified invertebrate samples.

Statement of Author contribution can be found in Appendix A.

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Chapter 1. General introduction

Aquatic ecosystems have been severely impacted by land-use and climate change (Strayer and Dudgeon, 2010; Death et al., 2015; Taniwaki et al., 2017). Intensive agriculture and land use conversion, and rapidly growing world population have caused increased water abstraction and nutrient loads from land into aquatic ecosystems (Selman and Greenhalgh, 2010). Climate-related impacts further deteriorate aquatic ecosystems via increased temperature, and the increasing frequency and magnitude of floods, and droughts (Strayer and Dudgeon, 2010). Increasing water temperature has been extensively studied with about 10,100 studies found in Google scholar up to 2015. However, studies on human and climate-induced changes in flow pattern have had much lower attention with approximately 4,420 studies on floods and 2,490 studies on droughts. The effects of current and projected changes to flow disturbances on aquatic ecosystems, therefore, require more investigation.

Anthropogenic impacts have already increased the frequency and magnitude of floods and/or extreme flood events (Brown et al., 2007; Death et al., 2015; O'Connor et al., 2015). Any changes to flow pattern can cause significantly negative impacts on stream biota, and may lead to species loss if those fauna do not have characteristics compatible with the new flow regime (Lytle and Poff, 2004; Dudgeon et al., 2006; Vandewalle et al., 2010). Additionally, these aquatic ecosystems have been degraded by increasing nutrient inputs (Allan, 2004; Morgan and Cushman, 2005; Strayer and Dudgeon, 2010). High nutrient levels are associated with the loss of biodiversity (Morgan and Cushman, 2005; Strayer and Dudgeon, 2010), a shift in community structure toward species that feed on algae, bacteria, and fungi (Gafner and Robinson, 2007; Matthaei et al., 2010), a reduction in recreational and amenity values, and an increase in the costs for drinking water treatment (Foote et al., 2015). The concurrent occurrence of both flood-induced and nutrient-induced stresses, therefore, likely pose an increasing threat to stream biota (Staudt et al., 2013; Death et al., 2015).

Biological traits have successfully discriminated the role of potential anthropogenic environmental drivers affecting invertebrate communities (Menezes et al., 2010; Statzner and Beche, 2010; Baird et al., 2011). Results from trait analysis can easily transfer findings from one region or country to another thus the trait-based approach creates a comparative tool for environmental management over a range of scales that taxonomic analysis cannot offer (Dolédec and Statzner, 2010).

High flows physically remove individuals and periphyton biofilm, an important food source for many aquatic invertebrates (Scarsbrook and Townsend, 1993; Biggs, 1995; Death and Zimmermann, 2005). Benthic invertebrates possess characteristics or traits (e.g., streamlined bodies, flexible bodies, or small size) that help them maintain themselves in streams with high flows (Lake, 1990; Townsend et al., 1997a), avoid high discharge events (Wallace, 1990), or recolonize quickly after floods (Winterbourn, 1997). However, the trait-based approach has not been used to investigate the relative roles of physical removal and periphyton reduction in the overall effect of flood disturbance (Scarsbrook and Townsend, 1993; Townsend et al., 1997a).

Different flow regimes may select for distinctive trait composition of invertebrate communities because invertebrates that survive at a site are likely to have life history traits that reflect the timing, frequency, predictability and severity of flow regimes (Lytle, 2001; Lytle and Poff, 2004). However, the magnitude of change in the proportions of life history traits between flow regimes is typically small, namely less than 15% when trait proportions are compared between Mediterranean and temperate streams (Bêche et al., 2006; Bonada et al., 2007a; Bonada et al., 2007b). The small variation in trait proportions was probably associated with the single trait-based approach that has been commonly used in the literature (Bêche et al., 2006; Bonada et al., 2007a; Statzner and Beche, 2010). Environmental selective forces act on whole organisms with specific life history trait combinations rather than individual traits separately, such that life history traits are evolutionary auto-correlated (Poff et al., 2006; Verberk et al., 2013). Without considering phylogenetic linkages, results from the current trait-based approach might not be adequate to elucidate the overall response of traits to environmental changes (Poff et al., 2006; Verberk et al., 2013).

The effect of floods and spates on freshwater animals can be similar, regardless of their geographical location (Lake, 2000; but see Death and Barquín, 2012). Flow disturbances are the principal environmental factor shaping the diversity and community structure in Mediterranean and temperate streams (Chessman et al., 2010; Dolédec et al., 2017; Tonkin et al., 2017). Hydrological indices explain between 41% to 52% of the variation in invertebrate community composition in temperate New Zealand streams (Clausen and Biggs, 1997). However, it is still unclear exactly how flow disturbances structure tropical stream invertebrate communities (Boyero et al., 2009; Md Rawi et al., 2014; Tonkin et al., 2016).

Nutrient enrichment results in excessive epilithon growth that can shift community composition of invertebrate communities to those that fed on algae, bacteria and fungi, as well as decrease habitat quality by homogenizing invertebrate habitats, decreasing oxygen concentration and changing pH (Gafner and Robinson, 2007; Yuan, 2010; Lange et al., 2014). However, there is no study that has directly examined the effects of nutrient-induced changes in food sources on stream invertebrate traits (Matthaei et al., 2010; Lange et al., 2014).

The dual increases in flood-intensity and nutrient enrichment are likely to become more common (Staudt et al., 2013). Invertebrate communities can take three to ten years to recover after extreme floods (greater than 1-in-50 year events), whereas, it is typically a few weeks after smaller floods (Lake, 2008; Death et al., 2015; Reich and Lake, 2015). In contrast, a more rapid recovery of stream periphyton after floods at high nutrient level, may facilitate a quicker recolonization of invertebrate communities in nutrient-impacted streams (Biggs, 1995; Death and Zimmermann, 2005; Tonkin et al., 2013). Therefore, how these nutrient-enriched ecosystems respond to large floods still remains unclear (Death et al., 2015).

Thesis structure and aims

Questions to be investigated in this thesis include (i) how trait-based approaches can be used to study the effects of flow disturbance and nutrient enrichment on stream invertebrate communities, (ii) how flow disturbance and nutrient enrichment combine to effect stream invertebrate communities, and (iii) the effects of flow disturbances on stream invertebrate communities in tropical streams.

The trait-based analysis was used in Chapter 2, 3 and 4 to study the effects of flow and nutrient disturbance on trait composition of aquatic invertebrate communities in temperate streams. Chapter 5 used the taxonomic-based approach to investigate how different nutrient levels at differing flow disturbance levels influence invertebrate assemblages. Chapter 6 also used a taxonomic approach as there is a lack of Vietnamese trait data.

The objective of the main chapters in my thesis are as follows:

Chapter 2	Examine the relative importance of substrate disturbance and periphyton biomass removal on invertebrate traits in close-canopied sites and open-canopied sites in ten streams in Egmont National Park, New Zealand.
Chapter 3	Investigate whether the life-history strategies of invertebrate trait combinations, in 83 English and Welsh rivers are associated with patterns of river flow.
Chapter 4	Examine the effects of periphyton biomass, total nitrogen and dissolved reactive phosphate on functional feeding and life history traits of New Zealand stream invertebrates.
Chapter 5	Examine the recovery of invertebrate community composition from a 1-in-50-year event flood in Wellington, New Zealand. The study was conducted at five stream sites with contrasting nutrient concentrations from low to high nutrient concentrations.
Chapter 6	Examine the relationship between flow disturbance and diversity and community composition of invertebrate communities in Vietnamese mountain streams.

Chapter 2. Do disturbance and periphyton productivity affect stream invertebrate traits?

Authors: Yen T.H. Dinh and Russell G. Death

Affiliations: Innovative River Solutions, College of Science, Massey University, Private Bag 11-222, Palmerston North 4442, New Zealand

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Chapter 2. Disturbance – productivity effects on stream invertebrate traits

Abstract: Disturbance in lotic ecosystems strongly influences which animals can survive and how those ecosystems function. Flow disturbances physically remove animals and periphyton, but it is unclear whether physical removal of individuals or the loss of food is the principal driver of effects of flow disturbances on invertebrate communities. Invertebrates possess traits that help them withstand high flows or recolonize rapidly after floods. At light-limited, closed-canopy sites, periphyton biomass should be unaffected by disturbances, so disturbance should affect invertebrate community trait composition by direct removal of animals. At open-canopy sites, disturbance should affect trait composition by both removing individuals and reducing periphyton food resources. We investigated whether a trait-based approach could elucidate drivers of effects of flow disturbance on benthic invertebrate communities and better identify potential mechanistic linkages. We sampled 10 autotrophic streams that differed in substrate-disturbance regime and varied from 100 to 0% canopy cover. We sampled 2 sites per stream, 1 in forest (closed-canopy) and 1 downstream in low-intensity agricultural grassland (open-canopy). Regardless of canopy, in streams with greater substrate disturbance, the proportion of individuals that respired with a plastron increased and proportions of individuals having 2 aquatic life stages or who were filter-feeders decreased. At open-canopy sites, the proportion of collector-gathers with flattened bodies increased with increased substrate disturbance and decreased periphyton biomass, and the proportion of taxa having high body flexibility and 2 aquatic life stages increased with decreased substrate disturbance and increased periphyton biomass. Trait composition of these mountain stream invertebrate communities is strongly influenced by physical removal via substrate movement and by reduced periphyton resources.

Key words: invertebrate traits, flood disturbance, the loss of periphyton food, canopy cover.

INTRODUCTION

Floods can limit the distribution, abundance, and composition of animals in lotic habitats (Poff et al., 1997; Lake, 2000). Flood disturbance usually is characterized by the magnitude, frequency, duration, timing, and rate of change of flow (Poff et al. 1997). Any alteration to the magnitude or timing of flow can alter water chemistry, foodweb energy sources, physical habitats, and biotic interactions of aquatic ecosystems (Poff et al. 1997). As a result, flow alteration, particularly from anthropogenic causes, can cause significant negative effects on stream biota (Dudgeon et al., 2006; Poff et al., 2007) that may lead to species loss (Vandewalle et al., 2010).

High discharge usually results in decreased benthic invertebrate biomass, abundance, and richness (Lake, 2000; Robinson et al., 2003; Death, 2008). Floods increase shear stress on the stream bed, thereby causing substrate disturbance, which physically removes individuals (Townsend et al., 1997a; Death, 2002). A high proportion (70–95%) of individual invertebrates are removed by floods (Brooks and Boulton, 1991) despite the fact that benthic invertebrates possess characteristics or traits (e.g., streamlined bodies, flexible bodies, or small size) that help them maintain themselves in streams with high flows (Lake, 1990; Townsend et al., 1997a), avoid high discharge events (Wallace, 1990), or recolonize quickly after floods (Winterbourn, 1997).

Flow disturbances also remove periphyton, an important food source for many aquatic invertebrates (Scarsbrook and Townsend, 1993; Biggs, 1995; Death and Zimmermann, 2005). Death and Zimmermann (2005) found that a decline in the number of species with increased disturbance frequency occurred only at open-canopy sites where periphyton productivity was not light limited by a dense forest canopy. They postulated that diversity (richness) was reduced principally by removal of periphyton biomass—the disturbance–productivity–diversity model (Death 2002). However, exactly how high flows affect invertebrate communities is unclear.

Biological traits have been used successfully to discriminate the role of potential anthropogenic environmental drivers affecting invertebrate communities (Baird et al., 2008; Menezes et al., 2010; Statzner and Beche, 2010; Baird et al., 2011; Culp et al., 2011). Poff et al. (2010) used the traits, cold stenothermal and obligate rheophily, to assess the vulnerability of benthic communities to projected temperature and runoff change in the western USA. Communities at sites with taxa having a high proportion of these traits were deemed more vulnerable. Dolédec et al. (2011) found 9 traits linked with increasing agricultural intensity in New Zealand. The proportion of taxa laying eggs beneath the water surface increased and the number of taxa laying eggs at the water surface decreased with increasing agricultural intensity.

The relationships observed between traits and potential environmental drivers are relatively stable across large spatial scales (Culp et al., 2011; Dolédec et al., 2011). Thus, in contrast to taxonomic analysis, the trait-based approach creates a comparative tool for environmental management over a range of scales (Dolédec and Statzner, 2010). Dolédec et al. (2011) found that the responses of traits to agricultural intensification were consistent across New Zealand, even when taxonomic composition changed. Thus, traits offer the potential to transfer findings easily from one region or country to another.

Traits have rarely been used to explain the effects of flood disturbance on invertebrate communities, even in light of the potential effects that increases in large floods from climate changes may have on riverine biological communities (Death et al., 2015). Two studies have been done in which invertebrate traits were examined in relation to substrate disturbance (Scarsbrook and Townsend, 1993; Townsend et al., 1997a). Townsend et al. (1997) examined 6 selected traits in 54 tributary sites of the Taieri River on the South Island of New Zealand and found that taxa were small, habitat generalists, clingers, streamlined, or flattened, or had high adult mobility were more abundant at sites exposed to a high intensity of streambed substrate movement (Townsend et al., 1997a). However, the traits were not used in either study to investigate the relative roles of physical removal and periphyton reduction in the observed disturbance effects (Scarsbrook and Townsend, 1993; Townsend et al., 1997a). Therefore, whether removal of individual invertebrates and reduction of periphyton by disturbance have the same effect on traits in invertebrate communities affected by floods is unclear.

Autotrophic streams on Mount Taranaki in Egmont National Park, New Zealand, are covered by a full canopy of native evergreen forest and emerge from the park boundary into open pasture. The 10 studied streams are in the same geographical and geological region and have similar physicochemical characteristics, but differ in substrate disturbance regimes and vary from 100 to 0% canopy cover within a distance of few hundred meters (Death and Zimmermann, 2005). Five streams experience frequent flood disturbances, whereas the others are spring-fed and more stable. We took advantage of the differing substrate disturbance regimes and the differing limiting factors on periphyton accrual in these autotrophic streams to assess the relative contribution of the 2 potential driving factors on trait compositions. We investigated the ability of a trait-based approach to inform our understanding of the mechanisms of the effects of flow disturbance on benthic invertebrate communities by identifying: 1) the invertebrate traits associated with substrate disturbance, 2) the invertebrate traits associated with periphyton biomass, and 3) the invertebrate traits associated with both substrate disturbance and periphyton food loss.

METHOD

Study sites

We sampled 10 streams on the plain around Mount Taranaki, New Zealand, a dormant andesitic cone volcano. Mt Taranaki provides sites that are geographically close and of similar geological origin. A large portion of Mt. Taranaki is within the circular Egmont National Park, which is dominated by Rimu-Rata-Kamahi forest. The boundary of the national park is a sharp transition from forest to agricultural grassland, where forest canopy is almost completely absent. We sampled 2 sites on each stream, one ~50 m inside the forest and the other several hundred meters downstream in low-intensity agricultural grassland. Paired sites on each stream were 225 to 3800 m apart and differed significantly only in the presence or absence of forest canopy: sites inside the park are fully covered by forest canopy and paired lower sites are in open pasture with 0% canopy cover. All sites were ~400 to 500 m asl, 1^{st}- to 3^{rd}-order, and with similar physicochemical characteristics and substrate size composition (predominately large cobbles). All sites had annual mean water temperatures of 8 to 10°C and conductivity of 58 to 96 µS/cm (see Death and Zimmermann 2005 for more detail on study sites; Fig. 1A–G).

Invertebrate samples

We sampled invertebrates in April, July, October 1999 and January 2000. We collected five 0.1-m^2 Surber samples (250-µm mesh) from riffles at each site and stored them in 10% formalin. In the laboratory, invertebrates were removed from samples, identified to the lowest possible taxonomic level based on available keys, and counted (Cowley, 1978; Winterbourn et al., 1989; Towns and Peters, 1996). Those taxa that could not be identified to species level were separated into apparent morphospecies. Species abundance was the sum of individuals in the 5 Surber samples.

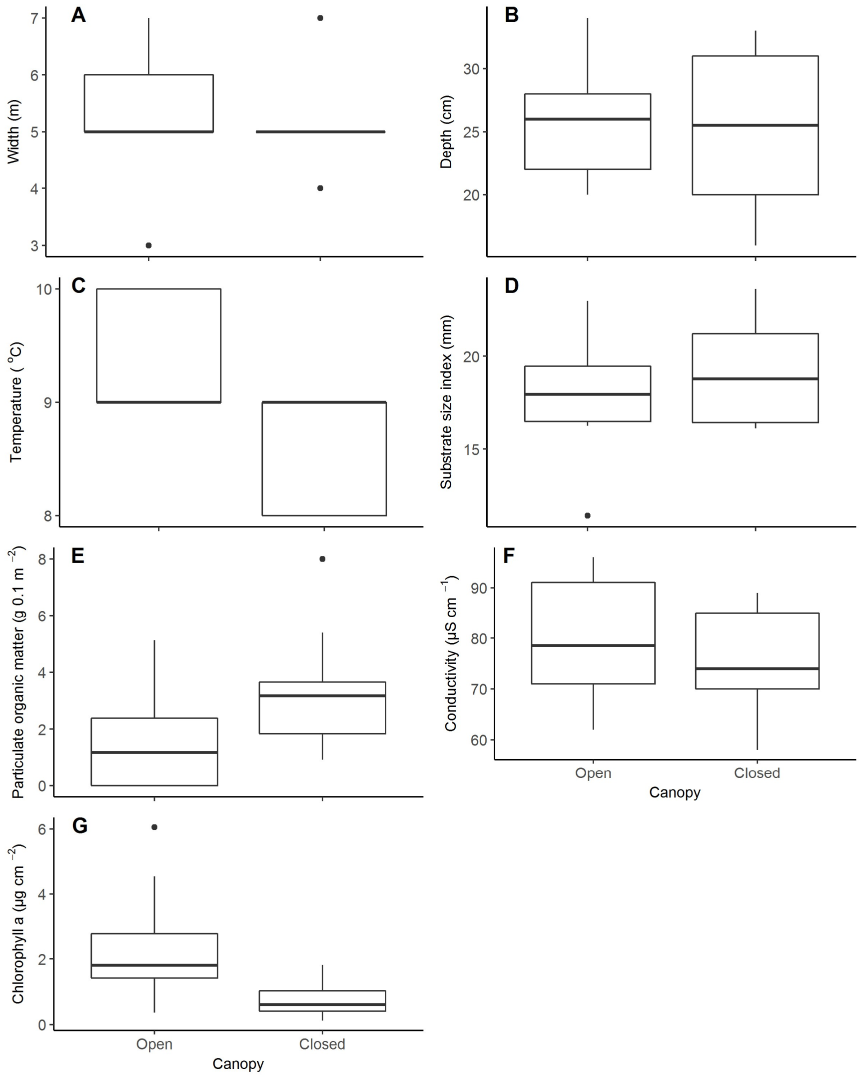

Figure 1. Box-and-whisker plots for stream width (A), depth (B), water temperature (C), substrate size index (D), particulate organic matter (E), conductivity (F), and chlorophyll *a* (G) at open- and closed-canopy sites 10 streams in Taranaki, New Zealand, in 1999–2000. Lines in boxes are medians, box ends are quartiles, whiskers are quartiles ± 1.5 * IQR (where IQR is the inter-quartile range), and dots are outliers.

Periphyton biomass

We assessed periphyton biomass by measuring chlorophyll *a* (Chl *a*). We collected 4 stones (maximum planar dimension < 60 cm) at random from riffles at each site monthly from April 1999 to January 2000, and kept them frozen. In the laboratory, we extracted pigments separately for each stone in known volumes of 90% acetone at 5°C in the dark for 24 h. We read absorbences with a Varian Cary (Melbourne, Australia) 50 UV Visible Spectrophotometer. Values were then converted to pigment concentration following Steinman et al. (2006). We corrected pigment concentrations for the stone surface area determined by wrapping stones in Al foil of known mass/unit area. We divided total surface area by 2 because periphyton generally is found only on the upper exposed surface of stones.

Substrate disturbance

We assessed the effect of disturbance on aquatic invertebrates by measuring substrate movement caused by high-discharge events in each stream. Subtrate movement was measured with the aid of 15 painted tracer particles placed on the stream bed (Death and Winterbourn, 1994b). We placed stones in each of 3 size classes (91–180, 61–90, and <60 mm) in riffles, in random order in triplets (small, medium, and large) across the main flow path of the stream at marked points on the stream bank at each stream. Every month between April 1999 and March 2000, we recorded the distance travelled by each stone, and we placed any stones that had moved back at their original position. We converted the sum of the distances moved to % stone movement by expressing it as a proportion of the maximum possible mass of stones moved (maximum possible mass of stones moved = 405.5 kg), thereby giving more emphasis to the movement of larger stones. A % stone movement of 100 indicates that all stones were washed away, buried, or moved >50 m, and a value of 0 indicates no stone movement. Substrate disturbance was measured at only the closed canopy site on each stream because of the close proximity of paired sites, the absence of any tributaries between paired sites, and their similar physical characteristics and channel morphology.

Selection of species traits

Fifteen feature groups with 50 trait categories have been identified for New Zealand freshwater invertebrates (Dolédec et al., 2011; Schmera et al., 2015). We selected 7 trait groups postulated to be linked with flow disturbance: number of aquatic stages, body flexibility, body form, mobility, dissemination potential, locomotion, potential size, and respiration (Townsend and Hildrew, 1994; Townsend et al., 1997a; Lamouroux et al., 2004; Horrigan and Baird, 2008; Statzner and Beche, 2010; Brooks and Haeusler, 2016); and 2 trait groups postulated to be related to periphyton abundance: dietary preference and feeding habit (Scarsbrook and Townsend, 1993; Brooks and Haeusler, 2016). Literature supporting their inclusion is listed in Table 1 along with our predictions of the trait responses to substrate disturbance or periphyton biomass based on that literature. We avoided, as much as possible, traits constrained by phylogeny (Poff et al., 2006) by excluding all life-history traits except maximum potential size. Taxa having small size are more resilient to flow disturbance than large taxa because of their short generation time (Townsend and Hildrew, 1994; Townsend et al., 1997b; Statzner and Beche, 2010).

Table 1. Predictions of trait linkages between substrate disturbance (F) and periphyton biomass (P) effects from flow disturbance made by other investigators.

Trait group/trait	Linkage	Strategies	Reference
Aquatic stages			
2 aquatic life stages	↓F	Longer time in water, higher chance to be exposed to high flows	Townsend et al. (1997)
1 aquatic life stage	↑F		
Body flexibility			
None (<10°)	↓F	Higher flexibility, quicker to find refuge from high flows	Townsend and Hildrew (1994), Lamouroux et al. (2004)
Low (>10-45°)	↓F		
High (>45°)	↑F		
Body form			
Streamlined	↑F	Streamlined or flattened body forms reduce drag force of high flows	Townsend et al. (1997), Statzner and Beche (2010)
Flattened	↑F		
Cylindrical	↓F		
Dissemination potential			
Low (<10 m)	↓F	Greater dispersal ability, higher capacity for intercatchment flight to avoid high flows	Townsend et al. (1997)
Moderate (10 m–1 km)	↓F		
High (>1km)	↑F		
Locomotion and relation to substrate			
Swimmers	↓F	Firmly attached to the substrate, less risk of being washed away by high flows	Townsend and Hildrew (1994), Horrigan and Baird (2008)
Crawlers	↓F		
Burrowers	↓F		
Attached	↑F		
Maximum potential size			
Small size (≤10mm)	↑F	Rapid recovery after disturbance, shorter generation time of smaller taxa	Townsend et al. (1997)
Large size (>10mm)	↓F		
Mode of respiration			
Tegument	↓F	Plastron or gill respirers can remain underwater indefinitely to avoid high surface flow	Brooks and Haeusler (2016)
Plastron	↑F		
Gills	↑F		
Dietary preferences			
Strong (specialist)	↓P	Generalists do not select their food, possibly feed on periphyton as an alternative food	Scarsbrook and Townsend (1993)
Moderate	↓P		
Weak (generalist)	↑P		
Feeding habit			
Scrapers	↑P	Scrapers feed on periphyton; deposit-feeders, filter-feeders, and collectors likely to be affected by high flows; response of scrapers to increased periphyton is likely to benefit predators	Scarsbrook and Townsend (1993), Brooks and Haeusler (2016)
Deposit-feeders	↓F		
Filter-feeders	↓F		
Collectors	↑F		
Predators	↑P		

Selection of analysis

Two common statistical tools for analyzing the relationship between traits and the environment are the fourth-corner problem proposed by Legendre et al. (1997) and the RLQ analysis proposed by Dolédec et al. (1996). These statistical tools possess some significant limitations, such as the analysis of a single trait and a single environment variable at a time and the impossibility of using abundance data (Menezes et al., 2010). These 2 limitations can be addressed by the fourth-corner model framework proposed by Brown et al. (2014), in which multiple traits expressed as a taxon-trait matrix, multiple environment variables expressed by a site–environment matrix, and abundance data expressed by a site–taxon matrix are integrated in the model-based analysis (Warton et al., 2015b).

Fourth-corner models use a direct 1-stage, model-based framework to fit abundance or presence/absence data against traits and environmental variables (Pollock et al., 2012; Brown et al., 2014). We kept each trait of each taxon as their original information rather than giving an affinity score based on fuzzy coding (Chevene et al., 1994), which is commonly used in the trait-based approach (Statzner et al., 2005; Bonada et al., 2007a; Dolédec et al., 2011; Pilière et al., 2015) and is the first key difference in the fourth-corner model approach (Brown et al., 2014). Considering abundance or presence/absence data rather than the weighted trait matrix as the response in the models is the 2nd key difference in the fourth-corner model approach (Brown et al., 2014). Thus, traits and environmental variables are linked directly in the models, which provides better quantification of relationships between traits and potential environmental variables. Fourth-corner models also allow users to check assumptions, quantify the nature and the strength of the environment–trait associations, identify the important associations, and forecast (relative) taxon abundance in new environmental scenarios (Brown et al., 2014;

Warton et al., 2015b), which similar analyses do not.

Data analysis

New Zealand invertebrate communities do not exhibit pronounced seasonal changes in abundance, so we did not consider seasonal patterns (Harding and Winterbourn, 1995; Suren and Jowett, 2006; Stark and Phillips, 2009). Death and Zimmermann (2005) found that flow disturbance at closed-canopy sites acted only by physically removing individuals, but flow disturbance at open-canopy sites removed both individuals and periphyton biomass. We analyzed data from open- and closed-canopy sites to partition the effects of animal removal and periphyton food resource removal. We removed rare taxa (those making up <5% of all individuals collected), early instar, and pupa data from the analysis. This step left 21 taxa at open-canopy sites and 23 taxa at closed-canopy sites for use in the analysis.

For each of the selected taxa, we used 9 feature groups (e.g., mode of respiration) with 28 traits (e.g., aerial, gills, plastron, and tegument) to describe the trait characteristics of the communities (Table 1). Trait information was generally coded at the generic level, with the exception of the family Hydraenidae (adult), which was coded at the family level. We obtained trait information from the New Zealand Invertebrate Trait database (NIWA, 2012).

We undertook all analyses with the *mvabund* package (version 3.11.4) in R (version 3.2.5; R Project for Statistical Computing, Vienna, Austria). We fitted models for substrate movement and periphyton biomass independently and separately at open- and closed-canopy sites. We used generalized linear models (GLMs) in the *traitglm* function to fit abundance of each taxon against substrate disturbance or periphyton biomass, traits, and their interactions, or environment-trait associations. The function uses multiple GLMs (multiGLMs), which are the extended form of multivariate linear models. The GLMs in the package *mvabund* are adapted for multivariate abundance data because they can be used with the strong mean–variance relationships and nonnormal data often found in ecology (Wang et al., 2012). A row effect was added in the *traitglm* model by applying the composition function (composition = TRUE) to adjust for different sampling intensities across different samples. This row effect can be understood as a compositional term in the sense that it models relative abundance at a site (Wang et al., 2012; Warton et al., 2015b).

The relationship between traits and environmental variables are described by interaction terms in the models as environment–trait associations (Brown et al., 2014; Warton et al., 2015b). We tested the significance of the environment–trait associations with the *anova.traitglm* function. This function used block resampling, in which sites were resampled but all species from a site were kept together in the resample (Warton et al., 2015b). The *p*-value was calculated from 999 iterative resamplings. p-values < 0.05 indicated significant trait–environment relationships. All assumptions for functions were checked and verified.

Traits linked specifically with substrate disturbance or periphyton biomass were identified by the model selection procedure by applying the Least Absolute Shrinkage and Subset Selection Operator (LASSO) penalty in the *traitglm* function. This penalty set to 0 any interaction coefficients that do not reduce the Bayesian Information Criterion (BIC) and returns the interaction coefficients of the important trait–environment associations (Brown et al., 2014; Warton et al., 2015b). All predictors were standardized, so the sizes of the coefficients measure the relative importance of the predictors (Warton et al., 2015b). Each interaction coefficient can be interpreted as the amount by which a unit (1 SD) change in the trait variable altered the slope of the relationship between abundance and the environmental variable of interest (Warton et al., 2015b). The magnitude and sign of the interaction coefficients indicated the strength and the direction of the effect of substrate disturbance or periphyton on traits. The higher the value of the interaction coefficients, the stronger the relationship between the traits, and substrate disturbance or periphyton.

RESULTS

Traits associated with substrate disturbance

Substrate disturbance affected traits regardless of whether the sites were in the open or under canopy ($p = 0.008$ at closed- and $p = 0.003$ at open-canopy sites) (Table 2). Three traits were linked with substrate movement at both open- and closed-canopy sites. Taxa having 2 aquatic life stages and who were filter-feeders had a negative association with more substrate movement (Table 3, Fig. 2A). Taxa that respired using a plastron were positively linked with more substrate disturbance (Fig. 2B). Nine traits were linked with substrate movement only at the closed-canopy site and 1 trait was linked only at the open-canopy sites. At closed-canopy sites, 6 traits were positively linked with greater substrate disturbance: small size, being a burrower, firm attachment to substrate, high mobility, inflexible bodies, and being a predator. Three traits were negatively linked: moderate mobility, being a swimmer, and being a deposit-feeder. At open-canopy sites, only being a scraper was positively associated with more substrate disturbance (Table 3).

Substrate disturbance had a stronger positive effect on traits at closed- than at open-canopy sites. The interaction coefficients of the associations between traits and substrate disturbance ranged from –0.16 to 0.19 at closed-canopy sites, and from –0.23 to 0.1 at open-canopy sites (Fig. 3).

Table 2. Analysis of deviance results testing the significance of interaction terms between substrate movement or periphyton biomass and traits obtained from the fourth-corner models. Samples were collected from open- and closed-canopy sites on 10 streams in Taranaki in 1999–2000. Res.Df = deviance of residuals, Df.dff = number of parameters taken up by interaction terms, and Dev = deviance. * = $p < 0.05$, ** = $p < 0.01$.

Model	Residual df	Interaction terms	Deviance	p
Closed-canopy sites				
Traits : substrate movement	876	19	106.4	0.008**
Traits : periphyton biomass	876	19	43.74	0.32
Open-canopy sites				
Traits : substrate movement	802	17	67.98	0.003**
Traits : periphyton biomass	702	17	55.07	0.01*

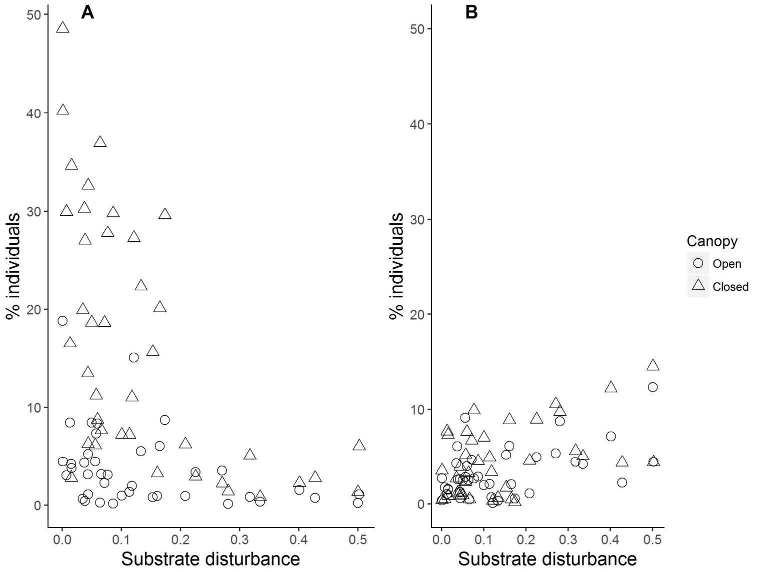

Figure 2. The proportion of individuals that were filter feeders having 2 aquatic life stages (A) and that used plastron respiration (B) and plotted against substrate disturbance at open- and closed-canopy sites on each sampling occasion at open- and closed-canopy sites in 10 streams in Taranaki, New Zealand, in 1999–2000.

Table 3. Traits associated with substrate disturbance or periphyton biomass. Traits in bold are those affected by substrate disturbances regardless of canopy cover or by both substrate disturbance and periphyton biomass at open-canopy sites. The interaction terms were selected by the Least Absolute Shrinkage and Subset Selection Operator (LASSO) penalty. The nature and the strength of the disturbance-trait associations are identified by the sign and magnitude of the interaction coefficients between substrate movement/periphyton biomass and the traits. Samples were collected from open- and closed-canopy sites on 10 streams in Taranaki in 1999–2000.

	Closed-canopy sites	Open-canopy sites	
Traits	Substrate disturbance	Substrate disturbance	Periphyton biomass
Plastron respirers	**0.15**	**0.07**	
Filter-feeders	**–0.13**	**–0.1**	
Two aquatic life stages	**–0.16**	**–0.13**	**0.04**
High flexible body		**–0.23**	**0.14**
Collectors		**0.1**	**–0.17**
Flattened body form		**0.02**	**–0.08**
Scrapers		0.01	
Dietary specialist			0.05
Predators	0.01		0.05
High mobility	0.005		
Moderate mobility	–0.04		
Deposit-feeders	–0.1		
Inflexible body	0.19		
Firm substrate attachment	0.08		
Burrowers	0.05		
Swimmers	–0.14		
Small size	0.02		

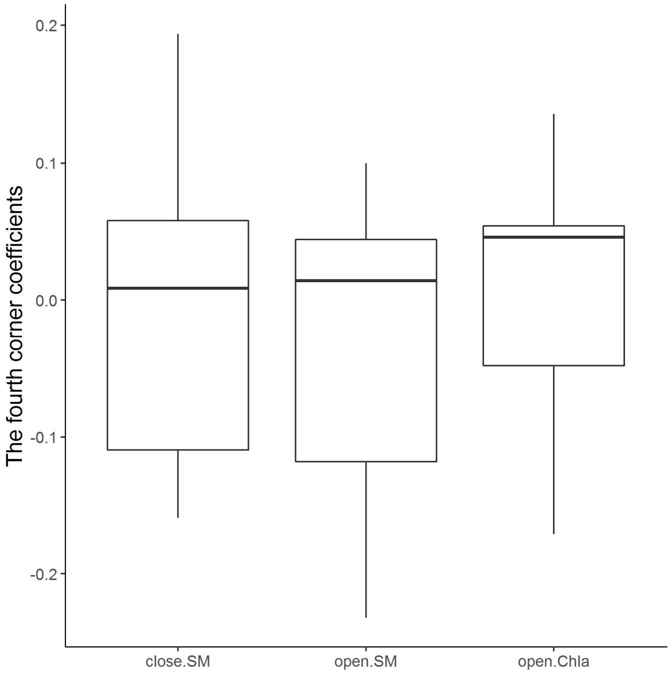

Figure 3. Box-and-whisker plot of the coefficients for interaction between traits and substrate movement at closed- (close.SM) and open-canopy (open.SM) sites, periphyton biomass at open-canopy sites (open.Chla), and substrate movement at open-canopy sites (open.SM) in 10 streams in Taranaki, New Zealand, in 1999–2000. The interaction terms were selected by the Least Absolute Shrinkage and Subset Selection Operator (LASSO) penalty for the fourth-corner models, from fitting abundance data to the environment and traits. Lines in boxes are medians, box ends are quartiles, and whiskers are quartiles ± 1.5 * IQR (where IQR is the inter-quartile range).

Traits associated with only periphyton biomass

Periphyton biomass was linked with traits only at open-canopy sites (Table 2). Two traits were positively linked with high periphyton biomass: dietary specialization and being a predator (Fig. 4). No trait was negatively associated with high periphyton biomass (Table 3).

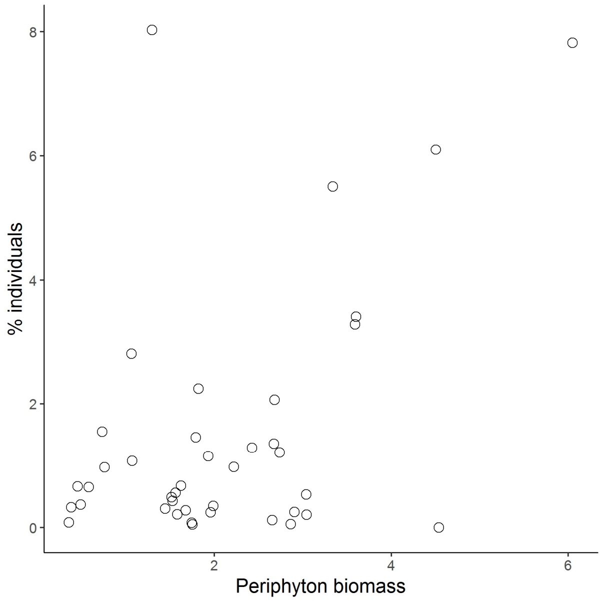

Figure 4. The proportion of predators plotted against periphyton biomass at open-canopy sites in 10 streams in Taranaki, New Zealand, in 1999–2000.

Traits associated with both substrate disturbance and periphyton biomass

The effects of both substrate movement and periphyton biomass on traits occurred only at open-canopy sites (Table 2). Two traits were positively linked with more substrate movement but negatively associated with high periphyton biomass: being a collector and having a flattened body (Table 3, Fig. 5A, B). Two traits were negatively linked with more substrate movement but positively associated with high periphyton biomass: having a flexible body and 2 aquatic life stages (Fig. 5C, D). Traits were more strongly associated with periphyton biomass than substrate movement. The median of the interaction coefficients of the associations between periphyton biomass and traits were higher than those between substrate disturbance and traits (Fig. 3).

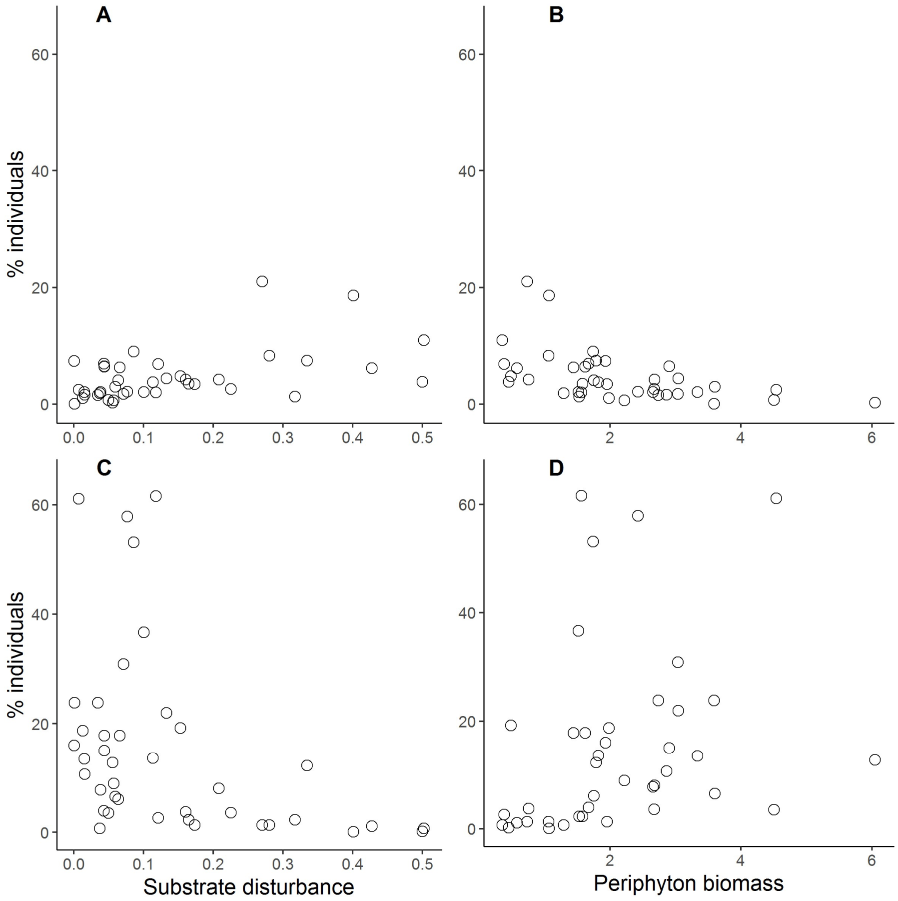

Figure 5. The proportion of collectors with flattened body form (A, B) and taxa with highly flexible body and 2 aquatic life stages (C, D) on each sampling occasion plotted against substrate disturbance (A, C) and periphyton biomass (B, D) at open-canopy sites in 10 streams in Taranaki, New Zealand, in 1999–2000.

DISCUSSION

The effect of flow disturbance on invertebrate traits

Flow disturbance can affect invertebrate traits through physical removal of individuals or loss of food. At closed-canopy sites, biomass of periphyton is strongly limited by the overhanging canopy and is unlikely to change with disturbance. Thus, disturbance should affect invertebrate trait composition only through the direct removal of animals. However, at open-canopy sites, both substrate disturbance and periphyton biomass can affect invertebrate trait composition. In our study streams, periphyton biomass was 3× higher at open- than at closed-canopy streams (Death and Zimmermann, 2005), and median interaction coefficients between traits and periphyton biomass were higher than those between traits and substrate movement. Food loss, therefore, appears to have a stronger influence on inverterbate traits than substrate disturbance, although both of them were important drivers of effects of high-flow disturbances on trait composition in the open-canopy streams.

Traits linked with substrate disturbance

Substrate disturbance affected invertebrate trait composition regardless of the presence of the overhead canopy. We considered traits indicative of substrate disturbance only if they were affected by substrate disturbance regardless of presence of overhanging cover because effects on traits that occurred only in the open-canopy streams could be a result of either physical removal or loss of periphyton food. These traits were using plastron respiration, having 2 aquatic life stages, and being filter-feeders

The observed response of individuals that respired using a plastron was positive at disturbed sites in both open- and closed-canopy streams. A plastron is an array of rigid, closely-spaced hydrophobic hairs (setae), which efficiently extract dissolved O_2 from water. A plastron is more resistant to physical damage during floods than unprotected gills (Flynn and Bush, 2008). Tomanova and Usseglio-Polatera (2007) also found that taxa with plastrons were more abundant in streams with high-flow disturbances.

The observed response of taxa with 2 aquatic life stages and those that are filter-feeders was negative at disturbed sites. Most aquatic insects have aquatic and terrestrial life stages. These taxa are likely to be more abundant at sites with less disturbance simply because the more time spent in the stream in flood-prone streams, the greater the chance of being exposed to destructive flows (Southwood, 1977; Townsend and Hildrew, 1994). The negative association between filter-feeders and substrate disturbance can be explained by their need for exposed attachment sites, which position them in places most affected by disturbance (Brooks and Haeusler, 2016). Individuals having both 2 aquatic life stages and being filter-feeders, therefore, were more abundant at less-disturbed sites.

Some traits were associated with substrate disturbance at sites with either open or closed canopy. At the closed-canopy sites, the positive response of individuals having small size, high mobility, or firm attachment and the negative response of those having moderate mobility, being a swimmer, and being a deposit-feeder were consistent with our prior predictions (Table 4). We were surprised that individuals with inflexible bodies were more abundant at disturbed sites, but these individuals (in our case: the cased caddisflies *Beraeoptera roria*) also were more common in disturbed than in undisturbed streams in taxonomy-based studies (Death, 2003). High abundance of individuals with inflexible bodies in streams with high levels of substrate disturbance is difficult to explain. We propose that the positive response of *B. roria* to substrate disturbance might be related to life-history traits that we did not consider in our study. Further studies, therefore, should be done to investigate the effects of substrate disturbance on invertebrate life-history traits. In addition, more burrowers occurred at disturbed sites than expected based on the literature (Lamouroux et al., 2004; Tomanova and Usseglio-Polatera, 2007). Burrowers typically are found in pool habitats in perennial streams (Walters, 2011). We suggest that pool habitat might act as an important refuge for burrowers during high flows, leading to the positive relationship between burrowers and disturbance in our study.

The positive response of scrapers to disturbance at only open-canopy sites probably reflected the response of the most dominant scraper (the mayfly *Deleatidium*) (Fig. 6). The similarity between the response of a single trait and groups that consist mostly of organisms that express the trait was expected (Pilière et al., 2015). The greater abundance of *Deleatidium* in disturbed than undisturbed streams might be associated their behavioural response of drifting during high-flow events, which would enhance their ability to recolonize quickly after substrate disturbance (Townsend et al., 1997a; Death, 2003). Therefore, the positive response of scrapers to substrate disturbance at open-canopy sites may be statistically but not ecologically significant. Our finding highlights the possibility of misinterpreting of environmental response of a single trait, especially if the trait occurs in a highly dominant taxon (Pilière et al., 2015).

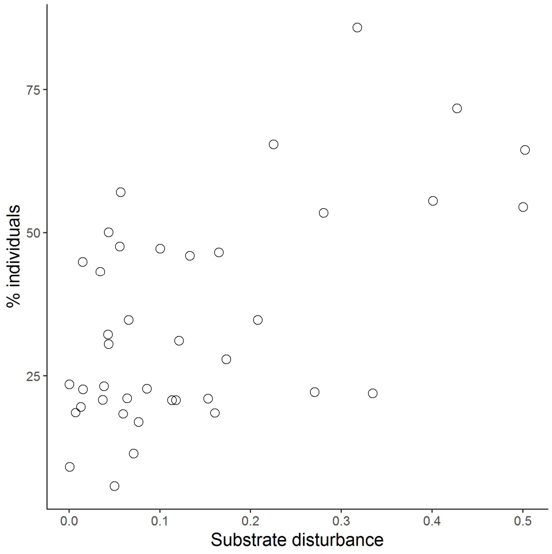

Figure 6. The proportion of *Deleatidium* spp. plotted against substrate disturbance on each sampling occasion at open-canopy sites in 10 streams in Taranaki, New Zealand, in 1999–2000.

Traits linked with only periphyton biomass

More periphyton biomass was positively linked with being a predator and being a dietary specialist. Predators are more abundant at sites with higher periphyton biomass because this biomass provides more food for their prey. The positive association between dietary specialists and periphyton biomass is mainly because the predators in our study were dietary specialists.

Table 4. Comparisons between predicted responses of invertebrate traits and flow disturbance (F) and periphyton biomass (P) and observed responses of invertebrate traits and substrate disturbance (SD) and periphyton biomass. Samples were collected from open- and closed-canopy sites on 10 streams in Taranaki in 1999–2000.

Trait group/trait	Predictions	Observed	Canopy
Aquatic stages			
2 aquatic life stages	↓F	↓SD	Both
1 aquatic life stage	↑F	ns	
Body flexibility			
None (<10°)	↓F	↑SD	Closed
Low (>10–45°)	↓F	ns	
High (>45°)	↑F	↓SD↑P	Open
Body form			
Streamlined	↑F	ns	
Flattened	↑F	↑SD↓P	Open
Cylindrical	↓F	ns	
Dissemination potential			
Low (<10 m)	↓F	ns	
Moderate (10 m–1 km)	↓F	↓SD	Closed
High (>1 km)	↑F	↑SD	Closed
Locomotion and relation to substrate			
Swimmers	↓F	↓SD	Closed
Crawlers	↓F	ns	
Burrowers	↓F	↑SD	Closed
Attached	↑F	↑SD	Closed
Maximum potential size			
Small size (≤10 mm)	↑F	↑SD	Closed
Large size (>10 mm)	↓F	ns	
Respiration of aquatic stages (not including eggs)			
Tegument	↓F	ns	
Plastron	↑F	↑SD	Both
Gills	↑F	ns	
Dietary preferences			
Strong (specialist)	↓P	↑P	Open

Trait group/trait	Predictions	Observed	Canopy
Moderate	↓P	ns	
Weak (generalist)	↑P	ns	
Feeding habit			
Scrapers	↑P	↑SD	Open
Deposit-feeders	↓F	↓SD	Closed
Filter-feeders	↓F	↓SD	Both
Collectors	↑F	↑SD↓P	Open
Predators	↑P	↑P	Open

Traits linked with both substrate disturbance and periphyton biomass

New Zealand streams have asynchronous and generally low levels of allochthonous inputs (Winterbourn, 1997). At open-canopy sites, high shear stress from flood events abrade periphyton biofilms that develop on stone surfaces, but algae persist in rock crevices and at low biomass on stone surfaces. Collectors having flattened bodies responded positively at more-disturbed sites even though periphyton food was limited. Horrigan and Baird (2008) found a positive relationship between the proportion of collector taxa and flow velocity. A flattened body reduces drag forces from high flows and enables these invertebrates to maintain themselves in the higher flows during floods. Townsend et al. (1997a) found a positive association between the proportion of individuals with flattened bodies and substrate disturbance.

Contrary to our expectations, we found a negative response of individuals with flexible bodies to disturbance (Table 4). Flexible bodies reduce shear stress from high flows, so taxa with this trait can survive in streams with frequent and intense floods. However, these taxa are unlikely to be excluded from less-disturbed streams (Hildrew and Giller, 1987; Townsend and Hildrew, 1994; Townsend et al., 1997a). Furthermore, a positive response of taxa spending longer in the stream at less- than at more-disturbed sites with open canopies was consistent with the pattern observed in the closed-canopy sites. As a result, individuals having both flexible body and 2 aquatic life stages responded positively at less-disturbed sites.

Our trait-based analysis explained flow-disturbance effects on community patterns observed by Death and Zimmermann (2005) in their taxonomically focused study. Filter-feeders having 2 aquatic life stages (the caddisflies *Orthopsyche* and *Aoteapsyche*) responded more positively at closed- than open-canopy sites, whereas positive responders at open-canopy sites had both highly flexible bodies and 2 aquatic life stages (chironomids and oligochaetes). These taxa were characteristic of closed- and open-canopy sites in the study by Death and Zimmermann (2005). Linking species traits with the observed species differences, therefore, helps clarify how high flows affect invertebrate communities.

To conclude, the principal driver of effects of flow disturbance on trait composition in the light-limiting New Zealand streams was removal of individuals. The loss of periphyton food seemed to be a more important driver of community changes associated with flow disturbances, but both disturbance and periphyton biomass significantly affected trait composition at streams without forest cover. At open-canopy sites, differences in the proportion of plastron respirers and filter-feeders probably reflected the effects of substrate disturbance because these traits were affected by disturbance regardless of canopy cover. On the other hand, differences in the proportion of collectors having flattened body form and those having highly flexible bodies probably indicated the combined effects of disturbance and loss of periphyton biomass. Thus, we were able to separate the influence of substrate disturbance from the combined effects at the open-canopy sites. However, we were unable to partition independent effects of each factor within the combined effects.

Chapter 3. The effects of flow regime on life history strategies of aquatic invertebrate communities.

Authors: Yen T. H. Dinh[1], Wendy A. Monk[2], Paul Wood[3] and Russell G. Death[1]

Affiliations:

[1] Innovative River Solutions, College of Sciences, Massey University, Private Bag 11-222, Palmerston North, New Zealand.

[2] Department of Biology, Canadian Rivers Institute, University of New Brunswick, Fredericton, New Brunswick, E3B 6E1, Canada.

[3] Department of Geography, Loughborough University, Loughborough, Leicestershire, LE11 3TU, UK.

Chapter 3. Flow regime affects life history traits

Abstract

Anthropogenically-modified flow regimes can dramatically change riverine community structure and function if life history traits of the local fauna are not compatible with the new flow regime. However, difference in proportions of individual life history traits between flow regimes is relatively small, less than 15% in the literature. This is probably associated with a single trait-based approach that is commonly used in current studies because that approach cannot account for phylogenetical auto-correlations between life history traits. We therefore investigated the composition of life history strategies, a combination of traits that is defined by evolutionary linkages, in 83 English and Wales rivers with three different flow regimes. Predictable multiple high flow events per year, characteristics of River type A, supported insects with strongly emergent synchronization in strategy S1 (median = 34.29%). The least variable flow due to strong groundwater influence in River type C had the highest abundances of non-flying invertebrates with strongly reproductive investment in strategy R3 (median = 36.34%), which characteristics were long-lived adults, large eggs and parental care. The modest flow variability characterized by a steep peak flow in River type B had an intermediate abundance of both strategy S1 and R3 (median = 25.05% and 21.6%, respectively). Different proportions in strategy S1 and R3 between River type A and C were 16.05 and 30.75%. The life history strategy approach, therefore, better reflected the responses of life history traits to flow regimes.

Keywords: body plans, discharge patterns, future flows, geographic constraints

INTRODUCTION

Ecological responses of biological river communities to flow alterations from anthropogenic impacts, including climate change and water resource management, are far from clear (Poff and Zimmerman, 2010; Death et al., 2015; O'Connor et al., 2015). Stream invertebrates in temperate areas may become extinct or immigrate northward while those in Mediterranean areas will move to the temperate areas as a result of an increased magnitude and frequency of floods and droughts across European in the context of climate change (Bonada et al., 2007a). The supradrought in Australia's Murray-Darling Basin between 1990 and 2009 reduced the prevalence of 11 invertebrate families; and they are yet to recover (Chessman, 2015).

Aquatic invertebrates that survive at a site are likely to have life history traits that reflect the timing, frequency, predictability and severity of flow regimes (Lytle, 2001; Lytle and Poff, 2004). Insects often enter the adult terrestrial phase and/or the diapause phase before flood or drought seasons, respectively. Many non-flying invertebrates (such as flatworms and leeches) enhance their fitness with synchronized reproduction when flows are optimal (Lytle and Poff, 2004). Any changes to flow pattern can, therefore, cause significant impacts on stream biota (Dudgeon et al., 2006; Poff et al., 2007) and may lead to species loss (Vandewalle et al., 2010) if life history traits of the local fauna are not compatible with the new flow regime (Lytle 2001, Lytle and Poff 2004).

Different flow regimes may select for distinctive trait compositions (Bêche et al., 2006; Bonada et al., 2007a; Statzner and Beche, 2010). Bonada et al. (2007b) found three trait groups characterised for three flow categories in the Mediterranean climatic area. They found that intermittent streams were dominated by taxa having reproduction by clutches, winged forms, aerial respiration, and swimmers. Ephemeral streams were dominated by taxa having reproduction by eggs or asexually, aquatic forms, tegument respiration, and substrate attachment. Perennial streams had a mixture of both trait groups (Bonada et al., 2007b). Highly predictable seasonal intermittent flows in Mediterranean streams favour taxa of a small size, aquatic adults, winged life stages and a swimming locomotion; whereas, less variable flows and intermittent flows in temperate streams support taxa having an intermediate size, aquatic larva, and a crawling locomotion (Bonada et al., 2007a). However, difference in proportions of life history traits between these flow regimes is typically small, less than 15% in the literature (Statzner et al., 2004; Bêche et al., 2006; Bonada et al., 2007a).

The single trait-based approach that is commonly used in the literature typically analyses individual trait performance assuming identical adaptive value of particular traits across species (Bêche et al., 2006; Bonada et al., 2007a; Bonada et al., 2007b). Analysing changes in life history traits associated with changing flow regimes needs to consider evolutionary inter-relationships because these traits are phylogenetically auto-correlated (Poff et al., 2006). The individual trait-based approach may, therefore, fail to identify an adaptive value of an animal having a particular life history trait combination (Poff et al., 2006). This might explain why differences of individual traits associated with changing flow regimes reported in the literature have been small (Statzner et al., 2004; Bêche et al., 2006; Bonada et al., 2007a).

A life history strategy approach proposed by Verberk et al. (2008b) grouped invertebrates into 13 strategies based on evolutionary linkages between traits. Therefore, these strategies may better describe associations between life history traits and flow regimes (Poff et al., 2006; Verberk et al., 2013). We thus studied the trait composition of invertebrate communities in 83 English and Welsh rivers using the life history approach. Monk et al. (2006) characterised the long-term flow regimes of these rivers into three distinctive types and found that Lotic-invertebrate Index for Flow Evaluation (LIFE;

Extence et al. (1999)) scores significantly differed among river types (Monk et al., 2007). River type A had multiple predictable high flows, river type B had a steep flow peak, and river type C had a prolonged rising climb with major groundwater aquifers (Monk et al., 2006).

METHOD

The distribution of river types

Monk et al. (2006) classified the flows of 83 streams in England and Welsh into three river types based on the form and timing of the annual hydrograph discharge pattern. Daily hydrological data recorded by the Environment Agency of England and Wales between 1980 and 1999 formed the base for the regime classification. Sites within River type A exhibited three high flow events per year (in October, December and March) and were located on impermeable geology in the wetter northwest of England and one site in south Wales (higher elevation streams). River type B sites exhibited one steep, high flow event in January and was located throughout north-eastern, central and southern England over a range of geologies. Sites within River type C exhibited a prolonged rising climb in March and were associated with major groundwater aquifers and mainly located in eastern and southern England (for more details refer to Monk et al., 2006).

Sample collection

Benthic invertebrate samples were paired with adjacent hydrological gauging stations. Biomonitoring samples were collected using a standard Freshwater Biological Association net using a three-minute kick sample (<1 mm mesh net) with an additional one-minute hand search, requiring collectors to sample instream habitats in proportion to their occurrence. Samples were collected annually between September and November from 1989 to 2000 before being identified to family-level where abundance data were recorded in $\log_{10}$ abundance categories (for more details refer to Monk et al., 2006).

Data analysis

Each taxon was assigned to a life history strategy based on the defined species traits in each of those strategies (Table 1 and Appendix S1). Trait information and strategies were obtained from Tachet et al. (2010), Verberk et al. (2008a), Poff et al. (2006), and Vieira et al. (2006). Invertebrates were identified to family level, except for non-insects that were recorded to order. When a family exhibited multiple traits, we defined the trait of the family as the trait of the most common genera. We then calculated the abundance of each strategy at each site by summing abundance of all families within that strategy. Samples collected at each site in different years were treated as replicates.

We undertook all analyses with the *mvabund* package (version 3.11.4) in R (version 3.2.5, R Project for Statistical Computing, Vienne, Austria). We used generalized linear models (GLMs) in the *mvabund* function to fit abundance of each strategy against the three river types (Wang et al., 2012). The function uses multiple GLMs (multiGLMs), which are the extended form of multivariate linear models. The GLMs in the package *mvabund* are adapted for multivariate abundance data because they can be used with strong mean–variance relationships and non-normal data that is often found in ecology (Wang et al., 2012). We added a row effect in the model to account for the resampling of each site. We tested the significance of the river type–strategy associations with the *anova.manyglm* function (Wang et al., 2012). We then obtained the p-value of each strategy by adding *p.uni=adjusted* in the *anova.manyglm* function (Wang et al., 2012) and then selected strategies whose *p*-value ≤ 0.05. The *p*-value was calculated from 999 iterative re-samplings. *p*-values < 0.05 indicated significant river type–strategy relationships. All assumptions for functions were checked and verified.

Table 1. Characteristics of the eight life history strategies used in our study. Trait information and strategies were obtained from Tachet et al. (2010), Verberk et al. (2008a), Poff et al. (2006), and Vieira et al. (2006).

Life history	Characteristics
D1	Active flight, strong dispersal, short development time, long-lived adults, mainly multi-voltine and large clutch size.
D2	Active flight, strong dispersal, short-lived adults, univoltine, and large clutch size.
D3	Active flight, weak-moderate dispersal, short-lived adults, mainly multi-univoltine, and early age at first reproduction.
R1	Active flight, weak-moderate dispersal, long-lived adults, sequential reproduction, rapid juvenile development
R2	No flight, short-lived adults, sequential reproduction with many small eggs, slow juvenile development, and high clutch size.
R3	No flight, long-lived adults, sequential reproduction with large egg size, parent care
R4	No flight, short generation time, asexual propagation and resistant stages
S1	Active flight, weak-moderate dispersal, short-lived adults, strong synchronised adult emergence and mainly univoltine.
S2	Active flight, weak-moderate dispersal, long-lived adults, mainly multivoltine, effectively synchronised adult emergence and resistant diapausing stage.
S4	Active flight, weak-moderate dispersal, long-lived adults, short synchronized juvenile development
T1	Active flight, weak-moderate dispersal, small size, and highly tolerant to harsh environment.
T2	No flight, long-lived adult, asexual reproduction, highly tolerant to long periods of harsh environment.

RESULTS

Strategy composition differed between the three river types, especially abundance of six life history strategies D1, D3, R3, S1, S2 and T2 (Table 2 and Fig. 1). River type A had a low abundance (median = 5.59%) of strategy R3 and a high abundance (median = 34.29%) of strategy S1. River type C had a high abundance (median = 36.34%) of strategy R3 and a low abundance (median = 18.24%) of strategy S1. An intermediate abundance of strategy S1 and R3 (median value 25.05% and 21.6%, respectively) characterized river type B. River type A had higher abundance of strategy D3 and T2, whereas, river type B and C had higher abundance of strategy D1 and S2 (Fig. 2).

Table 2. Results of analysis of deviance from the *anova.manyglm* function testing for a significant difference of life history strategies between river types. Data were collected in 83 English and Welsh rivers between 1989 and 2000. The global p value was given for the life history strategy composition. Each life history strategy was given a p value indicating whether its abundance differed significantly between the three river types. *** = $p \leq 0.001$; ** = $p<0.01$.

	df	Deviance	p
The strategy compositions	2	215.5	0.001***
Each life history strategy			
D1	2	48.73	0.001***
D2	2	4.7	0.39 ^{ns}
D3	2	30.87	0.001***
R1	2	7.62	0.23 ^{ns}
R2	2	10.35	0.17 ^{ns}
R3	2	53.57	0.001***
R4	2	1.56	0.5 ^{ns}
S1	2	34.94	0.001***
S2	2	36	0.001***
S4	2	7.04	0.23 ^{ns}
T1	2	8.06	0.22 ^{ns}
T2	2	20.59	0.01*

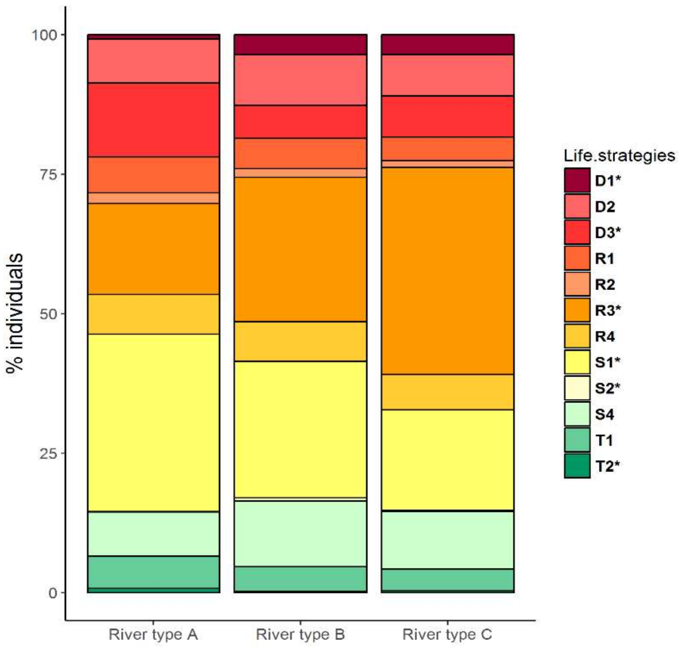

Figure 1. Histogram of percentage of individuals in each life history strategy in three river types collected in 83 English and Wales rivers between 1989 and 2000. * = life history strategy that relative abundance significantly differed between three river types ($p < 0.05$). Their p values were obtained by adding *p.uni=adjusted* in the *anova.manyglm* function (See detail in Table 2).

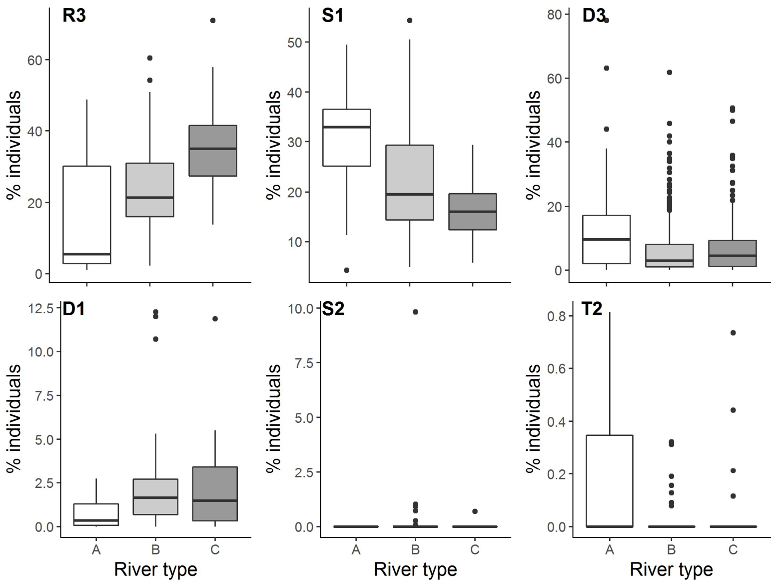

Figure 2. Box-and-whisker plots of the percent of individuals in each life history strategies that differed between river types in 83 UK rivers between 1989-2000. Lines in boxes are medians, box ends are quartiles, whiskers are quartiles ± 1.5*IQR (where IQR is the inter-quartile range), and dots are outliers.

DISCUSSION

The three river types supported different life history strategies. Similar to our findings, Zuellig and Schmidt (2012) found life history traits varied across nine eco-regions identified by climatic, physiographic and hydrological data in the United States. Poff et al. (2010) also found three trait community types for invertebrates in 279 western United States rivers in response to hydrological and climatic variables.

Multiple predictable high flow events, characteristics of River type A, supported highly synchronized strategy S1 because the strong synchronized adult emergence allows these invertebrates to escape from streams before high flow events, as long as those high flows are predictable (Lytle, 2001). It may explain the dominance of strategy S1 found in River type A sites. Traits characterized in strategy S1 were similar to trait characteristics in rivers with predictable floods of Western Mountain, US (Zuellig and Schmidt, 2012). Furthermore, invertebrates in highly tolerant strategy T2 can be tolerant to long periods in a harsh environment, such as multiple high flows in River type A, due to asexual reproduction and the lack of synchronized development in juveniles (Verberk et al., 2008b). This could contribute to a higher abundance of individuals in strategy T2 in River type A. Additionally, weak flyers with short-lived adults in strategy D3 would better suit River type A sites because these sites were restricted in high elevation areas (Monk et al., 2006; Sarremejane et al., 2017). As a result, characteristics of River type A resulted in the dominance of insects with strongly emergent synchronization in strategy S1 and higher abundances of insects with high tolerance in strategy T2 and D3.

In contrast, the least variable flows associated with strong groundwater influence in River type C were better for greater investment in reproduction of strategy R3 because these non-flying invertebrates can spread reproductive effort over a longer period and invest in parental brood care to increase the survival rate of their offspring (Verberk et al., 2008b). Spreading reproductive effort can give their offspring a competitive advantage over other species if they occupy more benign environments in River type C (Townsend and Hildrew, 1994; Verberk et al., 2008b), leading to the dominance of strategy R3 in River type C sites. Therefore, strong groundwater influence, characteristic of River type C, supported the dominance of non-flying invertebrates with highly reproductive investment in strategy R3.

The moderately variable flows in river type B supported life history investments in both synchronization and reproduction. The strongly synchronized adult emergence would benefit insects in strategy S1 from a predictable and steep high flow in River type B. An intermediate period of stable flow in River type B might be associated with an intermediate abundance of strategy R3 because these animals need stable flow to reproduce efficiently. Additionally, summer droughts are more common in River type B than River type A because of the wetter weather in the northwest of England, and rare in River type C because of the ground water influence (Monk et al., 2006; Monk et al., 2007). Summer droughts supported higher abundances of invertebrates in strategy S2 and D1 in River type B sites. Summer droughts would benefit strategy S2 because these insects have resistant diapause stages, either as eggs or aquatic adults, allow species to bridge long periods of unfavorable conditions in summer droughts (Verberk et al., 2008b). Similarly, summer droughts would benefit strategy D1 because these invertebrates spend most of their lifetime outside of rivers, reducing opportunities to be exposed to droughts (Townsend and Hildrew, 1994; Townsend et al., 1997a; Verberk et al., 2008b). Consequently, the moderate flow variability in River type B supported the dominance of invertebrates in both synchronized strategy S1 and reproductive strategy

R3 while more common summer droughts supported higher abundances of invertebrates in strategy S2 and D1.

We found relatively large differences in the proportions of strategies S1 and R3 between the three different hydrological river types. Median values for the proportions of strategies S1 and R3 between river types A and C were 16.05 and 30.75%. Previous studies found less than 15% proportional differences in life history traits in 384 running water sites across 14 European biogeographical regions and 527 reference-condition sites of Mediterranean and temperate regions in South Europe, Middle East and North Africa (Statzner et al., 2004; Bonada et al., 2007a; Bonada et al., 2007b). Flow variability differences between river types in our study were much less pronounced than those in previous studies (Monk et al., 2007). However, proportional differences in strategy S1 and R3 between river types A and C were much larger than differences in traits found between rivers of different flow typology in previous studies. We, therefore, conclude that the life history strategy approach improved the power to link traits with flows (Verberk et al., 2008b; Verberk et al., 2013).

The life history approach appeared to better describe differences in trait composition of invertebrate communities between flow regimes. This supported the view that environmental selective forces act on whole organisms via trait combinations that represent an adaptive value to environmental gradients rather than individual traits acting separately (Poff et al., 2006; Verberk et al., 2013). Combination of traits, therefore, likely have greater fitness than the individual trait separately (Verberk et al., 2013). The life history approach that integrate evolutionary inter-relationships between traits seemed to better describe differences in trait composition of invertebrate communities along environmental gradients than the single trait-based approach.

Chapter 4. The effects of nutrient enrichment on invertebrate traits in New Zealand streams

Authors: Yen T.H. Dinh and Russell G. Death

Affiliations: Innovative River Solutions, College of Science, Massey University, Private Bag 11-222, Palmerston North 4442, New Zealand

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Chapter 4. Nutrients affect invertebrate traits

Abstract

Eutrophication from land-use intensification can decrease biodiversity and ecological health in rivers. Nutrients affect invertebrates by altering the quality and quantity of food and modifying habitats because epilithon overgrows the substrate. The response of invertebrates, judged by changes in functional feeding traits to nutrient enrichment, appears equivocal in the current literature. However, no study has directly examined the effects of nutrient-induced changes in food sources on stream invertebrate traits. We used fourth corner models to assess the effects of periphyton biomass, total nitrogen, and dissolved reactive phosphate on life history and functional feeding traits in invertebrates collected in 17 New Zealand streams. Periphyton biomass and nutrients had similar effects on functional feeding and life history traits. The responses of shredders more likely reflected nutrient effects on food source, whereas, the responses of algae piercers reflect both food source and habitat changes. Collectors and scrapers having different life history traits responded differently to periphyton biomass and nutrients. As a result, both functional feeding and life history traits are important in monitoring nutrient effects on stream invertebrate communities. Evaluating invertebrate responses to nutrients may be sufficient to reflect the effects of nutrient-induced changes in periphyton biofilm on stream communities.

Keywords: Nutrient enrichment, periphyton overgrowth, trait combinations, stream invertebrates.

INTRODUCTION

Many of the world's waterways have been degraded by increased nutrient inputs from agriculture and urbanisation (Quinn, 2000; Allan, 2004; Strayer and Dudgeon, 2010). Nitrogen and phosphorus are the two most deleterious and ubiquitous of those nutrients (Carpenter et al., 1998; Elser et al., 2007). High nutrient levels are associated with a loss of biodiversity (Morgan and Cushman, 2005; Strayer and Dudgeon, 2010), and a shift in community structure of consumers (Gafner and Robinson, 2007; Matthaei et al., 2010). There are also reductions in the recreational and amenity value of waterways as well as increased costs for drinking water treatment (Foote et al., 2015). Eutrophication, therefore, not only reduces the ecological health of rivers and streams, but can also generate serious financial and social cost for many nations (Pretty et al., 2003; Dodds et al., 2009; Jarvie et al., 2013).

Nutrient enrichment can change the type of invertebrates that occupy a stream, particularly the composition of functional feeding and life history traits, by promoting epilithon overgrowth on the substrate. An increased biomass and productivity of epilithon biofilm can shift the invertebrate community composition to those that fed on algae, bacteria and fungi (Gafner and Robinson, 2007; Matthaei et al., 2010; Liess et al., 2012). Lange et al. (2014) found that abundances of scrapers, deposit feeders and predators were mostly strongly associated with the concentration of total nitrogen in waterways when evaluating changes in 52 biological traits. Additionally, epilithon overgrowth can homogenize habitats, decrease oxygen concentration, and change pH (Yuan, 2010). This can lead to changes in life history traits with increased nutrients, such as the maximum number of reproductive cycles per year, life duration of adults, reproductive techniques and aquatic stages (Lange et al., 2014).

However, the links between nutrient concentration and functional feeding trait composition is inconsistent in the literature (Dolédec et al., 2006; Townsend et al., 2008; Matthaei et al., 2010; Statzner and Beche, 2010; Wagenhoff et al., 2012; Lange et al., 2014). Shredder abundance may decline relative to other functional feeding groups in streams of the Taieri River, South Island, New Zealand, but in mesocosm experiments with the same taxa, there was no effect of increased nutrients (Townsend et al., 2008). In contrast to the study of Lange et al. (2014), Wagenhoff et al. (2012) found no relationship between scarpers, deposit feeders and predators and nutrients in mesocosm experiments at the same location in South Island, New Zealand. It, therefore, remains unclear exactly how nutrients can affect functional feeding trait composition in stream invertebrate communities.

Environmental selective forces act on whole organisms with specific life history trait combinations rather than individual life history traits separately because these traits can be phylogenetically autocorrelated (Poff et al., 2006; Verberk et al., 2013). However, the current studies that investigated nutrient effects on trait composition only examined the response of individual life history traits at a time (Townsend et al., 2008; Matthaei et al., 2010; Lange et al., 2014). Without considering responses of multiple traits at a time, findings from these studies might be constrained by phylogenetic effects and could not be adequate to elucidate trait responses to nutrient changes (Poff et al., 2006; Verberk et al., 2013).

Nutrients affect invertebrates by promoting the growth of epilithon, except at very high concentrations when nutrients can be toxic (Yuan, 2010). However, we are not aware of any study that has directly examined the effects of changes in food resources on functional feeding and life history traits. The main food resource of invertebrates in open New Zealand streams is periphyton (Winterbourn et al., 1981; Winterbourn, 1997). We, therefore, examined how functional feeding and life history traits responded to changes in periphyton biomass and nutrients.

METHOD

Study sites and nutrient measurements

We sampled 24 sites in 17 streams in the Manawatu region, New Zealand. Total nitrogen (TN) and dissolved reactive phosphorus (DRP) were collected yearly using standard methods (APHA method) between 1999 and 2007 (Death and Death, 2008). Means of nutrient concentrations and numbers of samples per year at each site are presented in Table 1.

Table 1. Mean for TN and DRP collected at 24 sites on 17 streams in Manawatu, New Zealand between 1999 and 2007.

Site	DRP (mg/L)	TN (mg/L)	No. samples per year
Tamaki River @ Reserve	0.007	0.095	27
Tamaki River @ State Highway 2	0.008	0.500	28
Mangatainoka River @ Putara	0.003	0.020	21
Pohangina River @ Piripiri	0.005	0.049	27
Tokomaru River @ Horseshoe Bend	0.005	0.080	24
Oroua River @ Fielding Street	0.010	0.240	193
Pohangina River @ Raumai	0.012	0.080	24
Manawatu River @ State Highway 2	0.009	0.396	202
Oruakeretaki Stream @ State Highway 2	0.023	0.000	2
Raparapawai Stream @ Jacksons Road	0.030	0.150	2
Mangapapa Stream @ State Highway 2	0.024	0.900	24
Manga-atua Stream	0.031	0.270	30

Site	DRP (mg/L)	TN (mg/L)	No. samples per year
Manawatu River @ Hopelands	0.024	0.900	139
Porewa Stream @ Onepuhi Road	0.030	0.275	40
Waikawa Stream	0.027	1.350	24
Mangarangiora Stream	0.039	0.950	19
Mangatera Stream @ State Highway 2	0.066	0.435	34
Makino Stream @ South Street	0.043	1.700	12
Makaretu Creek @ Ballance Valley Road	0.069	1.137	80
Mangatera Stream @ Timber Bay	0.141	0.810	90
Mangaone Stream @ Milson Line	0.130	0.640	24
Oroua River @ Awahuri	0.101	0.530	147
Tutaenui Stream @ Curls Bridge	0.480	1.900	109
Mangapapa Stream @ Troup Rd.	0.024	0.900	24

Periphyton biomass

The periphyton biomass was assessed by measuring Chlorophyll *a* on five stones (maximum planar dimension <60 cm) collected yearly at random in riffles at each site between 1999 and 2007, and kept frozen. In the laboratory, pigments were extracted separately for each stone in known volumes of 90% acetone at 5°C in the dark for 24 hours. Absorbencies of the solution were read using a Varian Cary 50 UV Visible Spectrophotometer. Values were then converted to pigment concentration following Steinman et al. (2006). The pigment concentration was adjusted by dividing half of the stone surface area (calculated following Graham et al. (1988)) because periphyton is generally only found on the upper exposed surface of stones. The means of chlorophyll at each site were calculated and used for analyses.

Invertebrate samples

Invertebrate samples were collected in 2007. Five 0.1m^{2}Surber samples (250µm mesh) were collected from riffles at each site and stored in 10% formalin. In the laboratory, invertebrates were removed from samples, identified to the lowest possible taxonomic level using available keys (Cowley, 1978; Winterbourn et al., 1989; Towns and Peters, 1996) and counted. Those taxa which could not be identified to species level were separated into apparent morphospecies. Abundance per taxon was the sum of individuals of the five Surber samples. Any taxon recorded less than twice was considered a rare species and excluded from the data set.

Data analysis

For each taxon, we used ten traits in four life history feature groups (maximum number of reproductive cycles per year, life duration of adults, reproductive techniques and aquatic stages) and seven functional feeding traits (scrapers, shredders, algal piercers, filter-feeders, deposit-feeders, collectors, and predators) to describe the trait characteristics of the communities. Trait information was obtained from the New Zealand Invertebrate Trait database (NIWA, 2012). Trait information was generally at the generic level.

Fourth corner models use a direct 1-stage, model-based framework that can fit abundance data against multiple traits and multiple environmental variables (Pollock et al., 2012; Brown et al., 2014; Warton et al., 2015b). Analysing the original information of multiple traits of each taxon, rather than an affinity score based on fuzzy coding, is the first key difference of the fourth-corner models compared to the current trait-based approach (Brown et al., 2014). The second key difference in fourth corner models was that abundance data, rather than a weighted trait matrix, is the response in the models

(Brown et al., 2014; Warton et al., 2015b). Fourth corner models, therefore, can address two significant limitations of common trait-based analyses, that is, the analysis of a single trait and a single environment variable at a time and the impossibility of using abundance data (Dolédec et al., 1996; Legendre et al., 1997; Menezes et al., 2010). Additionally, multiple traits and environmental variables are linked directly in fourth corner models, which provide better quantification of relationships between traits and potential environmental variables. Being a model-based framework, fourth corner models also allow users to check assumptions, quantify the nature and the strength of the environment–trait associations, identify the important associations, and forecast (relative) taxon abundance in new environmental scenarios (Brown et al., 2014; Warton et al., 2015b), which similar analyses do not.

We undertook fourth corner models using *traitglm* function in the *mvabund* package (version 3.11.4) in R (version 3.2.5; R Project for Statistical Computing, Vienna, Austria). We used generalized linear models (GLMs) in the *traitglm* function to fit abundance of each taxon against chlorophyll a, TN or DRP, traits, and their interactions, or environment-trait associations. Functional feeding and life history traits were assessed independently. The function uses multiple GLMs (multiGLMs), which are the extended form of multivariate linear models. The GLMs in the package *mvabund* are adapted for multivariate abundance data because they can be used with strong mean–variance relationships and non-normal data often found in ecology (Wang et al., 2012). A row effect was added in the *traitglm* model by applying the composition function (*composition = TRUE*) to adjust for different sampling intensities across different samples. This row effect can be understood as a compositional term in the sense that it models relative abundance at a site (Wang et al., 2012; Warton et al., 2015b).

The relationship between traits and environmental variables are described by interaction terms in the models as environment–trait associations (Brown et al., 2014; Warton et al., 2015b). We tested the significance of the environment–trait associations with the *anova.traitglm* function. This function used block resampling, in which sites were re-sampled, but all species from a site were kept together in the re-sample (Warton et al., 2015b). The *p*-value was calculated from 999 iterative re-samplings; *p*-values ≤ 0.05 indicated significant trait–environment relationships. All assumptions for functions were checked and verified.

Traits linked specifically with chlorophyll a, TN or DRP were identified by the model selection procedure by applying the Least Absolute Shrinkage and Subset Selection Operator (LASSO) penalty in the *traitglm* function. Both functional feeding and life history traits were fitted in the *traitglm* function at a time. The LASSO penalty set to 0 any interaction coefficients that do not reduce the Bayesian Information Criterion (BIC) and returns the interaction coefficients of the important trait–environment associations (Brown et al., 2014; Warton et al., 2015b). The focus of the study is on analyzing the effects of nutrient-induced changes in food sources on invertebrate traits, therefore, we excluded four traits of having short-lived, sexual reproduction, being deposit feeders and/or filter feeders because they were linked with TN and/or DRP, but not chlorophyll a. All predictors were standardized, so the sizes of the coefficients measure the relative importance of the predictors (Warton et al., 2015b). Each interaction coefficient can be interpreted as the amount by which a unit (1 SD) change in the trait variable alter the slope of the relationship between abundance and the environmental variable of interest (Warton et al., 2015b). The magnitude and sign of the interaction coefficients indicate the strength and the direction of the effect of chlorophyll a, TN or DRP on traits. The higher the value of the interaction coefficients, the stronger these relationships are.

RESULTS

Functional feeding and life history traits were linked with both chlorophyll a and nutrients (Table 2). Associations between shredders and scrapers with chlorophyll a and two nutrients were negative, whereas, algal piercers and collectors were positively associated (Fig 1 and Table 3). Individuals having univoltine life cycles had a negative link with chlorophyll a, TN and DRP, while those having two aquatic life stages, being long-lived, and/or having hermaphroditic ability were positively associated. Individuals having asexual reproduction were negatively associated with chlorophyll a, but positively linked with TN (Table 3).

Table 2. Analysis of deviance testing the significance of interaction terms between Chlorophyll a (Chla), dissolved reactive phosphate (DRP), total nitrogen (TN) and functional feeding and life history traits obtained from fourth-corner models. Samples were collected at 24 sites in 17 streams in Manawatu, New Zealand in 2007. * = $p < 0.05$, ** = $p < 0.01$.

Models	Interaction terms	Deviance	p
Functional feeding traits : Chla	6	32.99	0.04*
Functional feeding traits : TN	6	47.75	0.005**
Functional feeding traits : DRP	6	29.12	0.05*
Life history traits : Chla	6	75.03	0.007*
Life history traits : TN	6	119	0.003**
Life history traits : DRP	6	85.86	0.006**

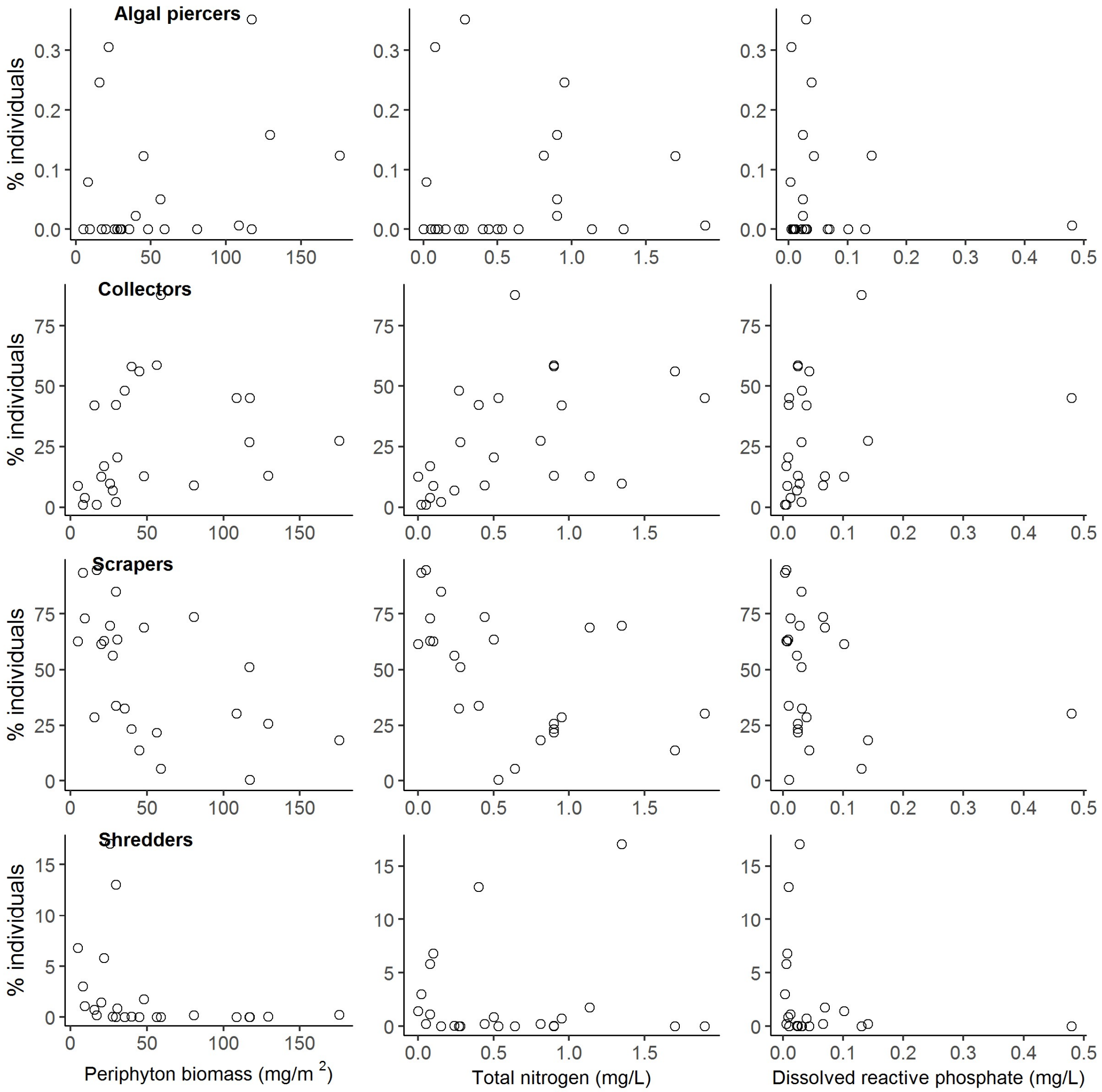

Figure 1. The proportion of algal piercers, collectors, scrapers and shredders plotted against periphyton biomass, total nitrogen, and dissolved reactive phosphate collected at 24 sites on 17 streams in Manawatu, New Zealand in 2007.

Table 3. Traits associated with Chlorophyll a (Chla), total nitrogen (TN) or dissolved reactive phosphate (DRP). The interaction terms were selected by the Least Absolute Shrinkage and Subset Selection Operator (LASSO) penalty. The nature and the strength of the disturbance-trait associations are identified by the sign and magnitude of the interaction coefficients between Chlorophyll a, total nitrogen (TN) or dissolved reactive phosphate (DRP) and invertebrate traits. Samples were collected at 24 sites on 17 streams in Manawatu, New Zealand in 2007.

Trait group/trait	Chla	TN	DRP
Life history traits			
Aquatic stages			
2 aquatic life stages	0.07	0.13	0.15
Life duration			
Long	0.09	0.01	0.06
Reproduction frequency			
Univoltine	-0.17	-0.30	-0.19
Reproduction technique			
Asexual	-0.2	0.07	0
Hermaphrodism	0.58	0	0.21
Functional feeding traits			
Algal piercers	0.04	0.05	0.03
Collectors	0.09	0.26	0
Scrapers	-0.1	-0.02	0.02
Shredders	-0.25	-0.18	-0.25

DISCUSSION

Associations between the responses of functional feeding and life history traits to periphyton biomass and/or nutrients were most likely a result of the link between periphyton biomass and nutrients (Fig. 2). This supports the idea that nutrients promote algal growth that, in turn, change the composition of functional feeding groups toward those that feed on algae (Matthaei et al., 2010; Yuan, 2010; Lange et al., 2014).

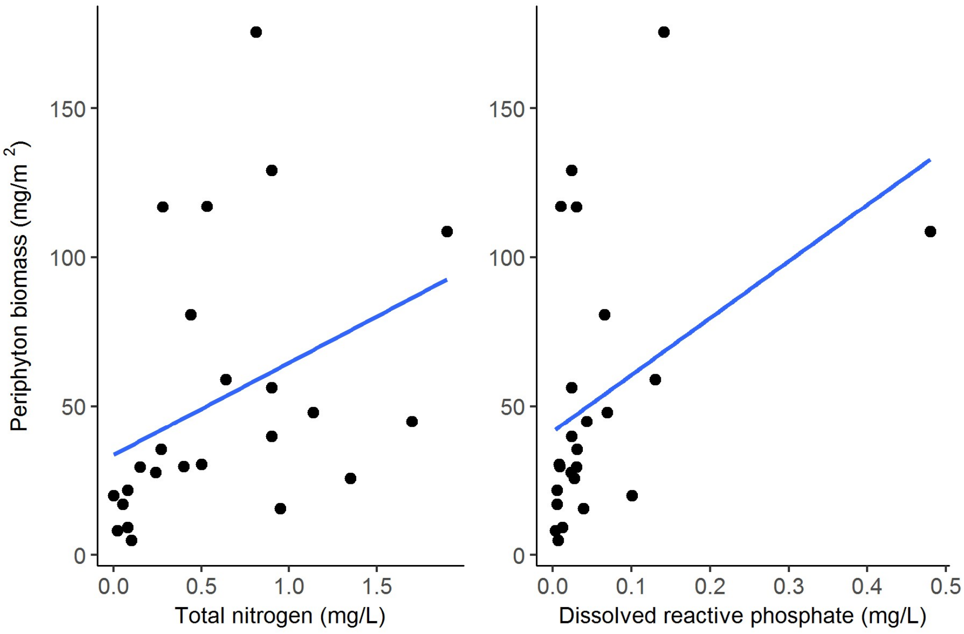

Figure 2. Periphyton biomass plotted against total nitrogen and dissolved reactive phosphate. Samples were collected at 24 sites on 17 streams in Manawatu, New Zealand in 2007.

Nutrient enrichment may shift algal communities from diatom dominance at low-nutrients to filamentous algae and cyanobacteria-dominated communities in high nutrient levels (Suren and Riis, 2010). Algal piercers directly feed on algae; therefore, a positive response of algal piercers with both periphyton biomass and nutrients was mostly because of an increased periphyton biomass at high nutrient levels. Two life history traits of having two aquatic life stages and being plurivoltine that showed a positive response to periphyton biomass and nutrients also contributed to higher abundance of algal piercers at high periphyton biomass. Therefore, the positive response of algal piercers likely reflected nutrient effects acting on both food source and habitat quality.

The increased periphyton biomass and nutrients resulted in a decrease in the abundance of shredders because they feed on coarse organic matter, which was consistent with the observed pattern in the study of Townsend et al. (2008) and Lange et al. (2014). Shredders have a wide range of life history traits that showed both negative and positive responses to periphyton biomass and nutrients. For example, the trait of having two aquatic life stages in the shredder caddisfly *Olinga feredayi* showed a positive response to periphyton biomass and nutrients, whereas, the trait of having one aquatic life stage in shredder stoneflies did not. Among these stoneflies, some are univoltine that showed a negative response to periphyton biomass and nutrients, whereas, others are plurivotine. While Hydraenidae beetles and the cranefly *Molophilus* have long-lived adults that showed a positive response to periphyton biomass and nutrients, other shredders have short-lived adults. Therefore, the negative response of shredders to periphyton and nutrients were mainly determined by nutrient effects acting on the food source.

The positive link between collectors and periphyton biomass and total nitrogen might be due to the fact that collectors feed on both streambed alage and other organic matter. Therefore, they can take advantage of a high abundance of streambed algae at high nutrient levels. However, we found that collectors being plurivoltine increased their abundance with periphyton biomass and total nitrogen, while those being univoltine decreased (Fig. 3 and 4). These different responses might be due to univoltine trait being negatively linked with periphyton biomass and nutrients, but the association with plurivoltine trait was positive. Collectors having different life history traits, therefore, reacted differently to periphyton biomass and nutrients.

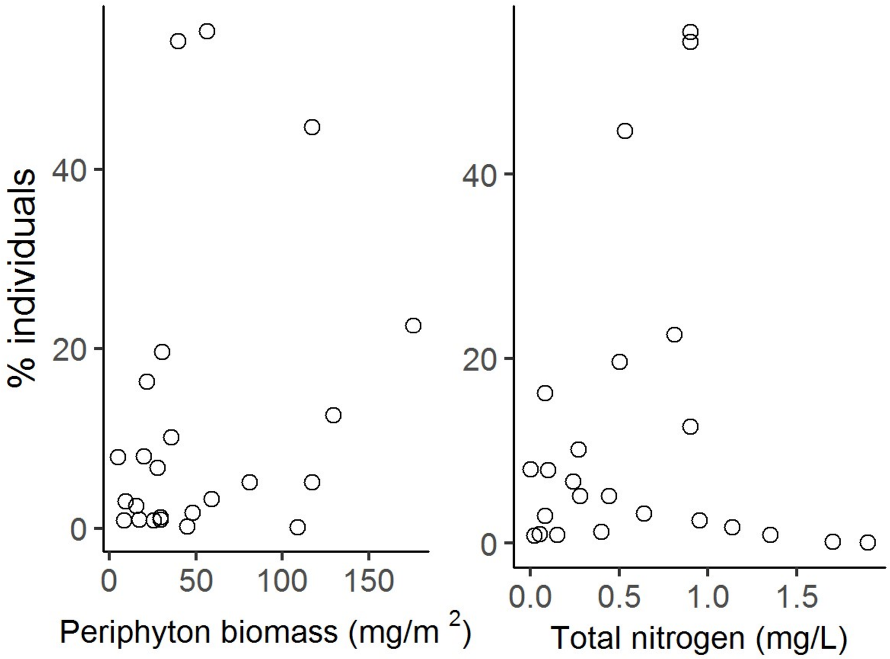

Figure 3. The proportion of collectors having plurivoltine plotted against periphyton biomass and total nitrogen collected at 24 sites on 17 streams in Manawatu, New Zealand in 2007.

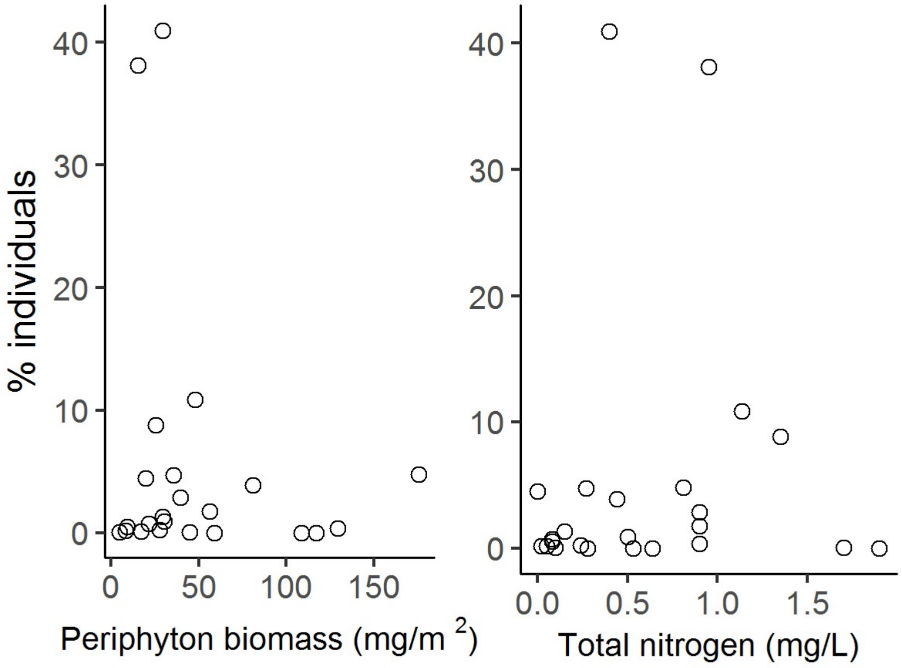

Figure 4. The proportion of collectors having univoltine plotted against periphyton biomass and total nitrogen collected at 24 sites on 17 streams in Manawatu, New Zealand in 2007.

The negative link between scrapers and periphyton biomass and total nitrogen was consistent with the finding of Lange et al. (2014). Filamentous algae and cyanobacteria mats at high nutrient levels are likely to be a poor habitat for many invertebrates including scrapers (Suren and Riis, 2010), leading to a decreased abundance of scrapers with increased periphyton biomass and nutrients. However, we found that scrapers having one aquatic life stage and sexual reproduction had decreased abundance with high periphyton biomass and nutrients while those having two aquatic life stages and hermaphroditic ability increased (Fig. 5 and 6). The traits of having two life stages in the stream and hermaphroditic ability but not those of having one life stage in water and sexual reproduction had a positive association with periphyton biomass and nutrients, leading to the contrasting responses of scrapers having these two trait combinations observed in our study. As a result, scrapers having different life history traits had different responses to periphyton biomass and nutrients.

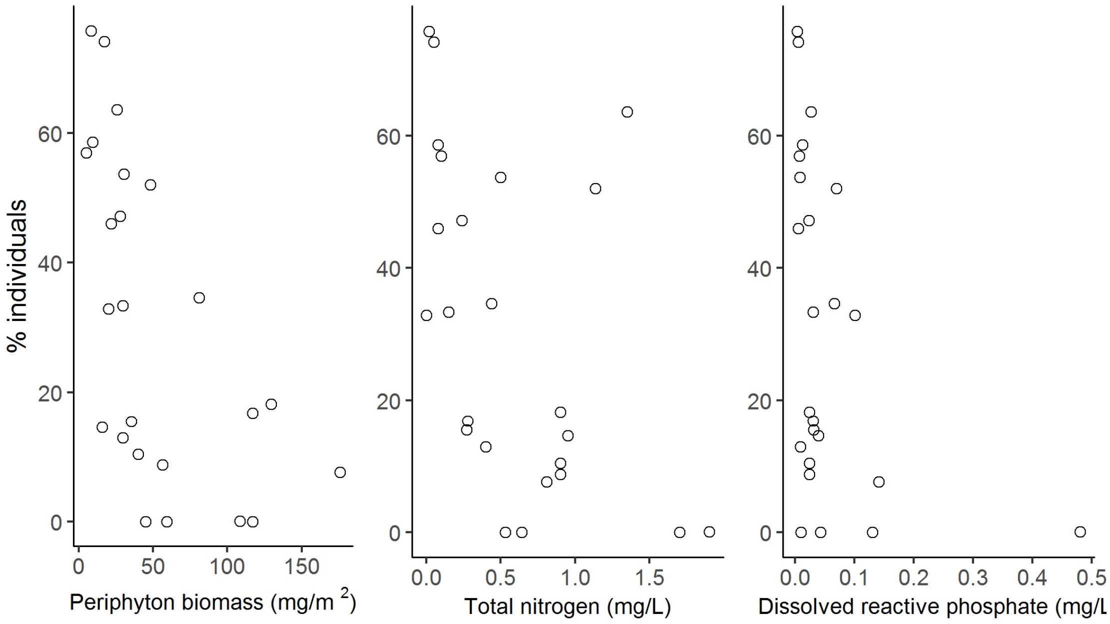

Figure 5. The proportion of scrapers having one life stage in water and sexual reproduction plotted against periphyton biomass, total nitrogen, and dissolved reactive phosphate collected at 24 sites on 17 streams in Manawatu, New Zealand in 2007.

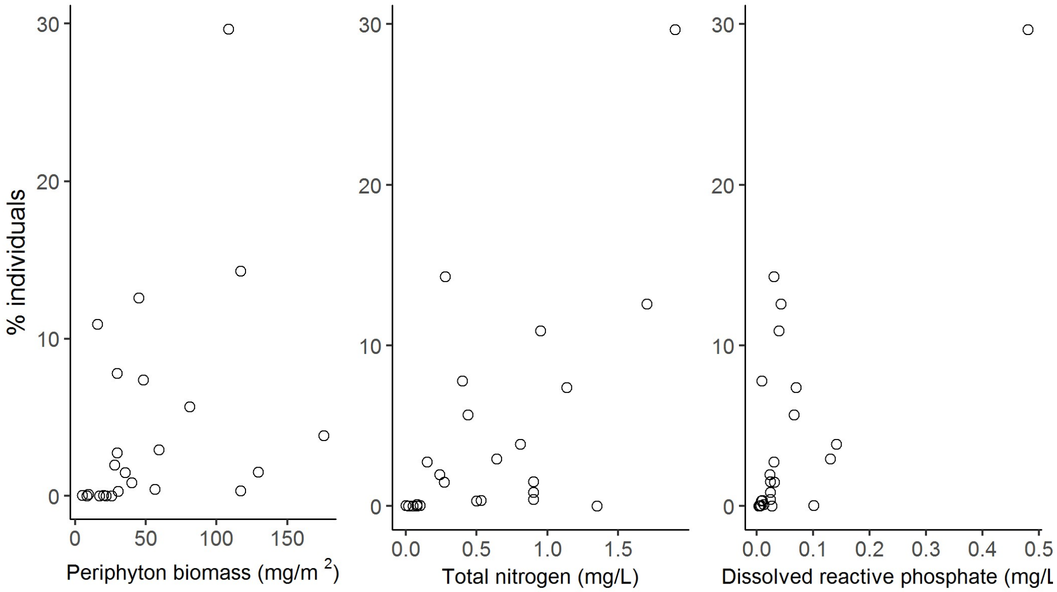

Figure 6. The proportion of scrapers having two life stages in water and hermaphroditic ability plotted against periphyton biomass, total nitrogen, and dissolved reactive phosphate collected at 24 sites on 17 streams in Manawatu, New Zealand in 2007.

Collectors being univoltine and scrapers having one aquatic stage and sexual reproduction decreased with increased periphyton biomass and nutrients, while collectors being univoltine and scrapers having two life stages in water and hermaphroditic ability, increased. Differences in life history traits of individuals having the same functional feeding traits may, therefore, explain the equivocal results of invertebrates to nutrient enrichment that have been observed elsewhere (Dolédec et al., 2006; Townsend et al., 2008; Matthaei et al., 2010; Statzner and Beche, 2010; Wagenhoff et al., 2012; Lange et al., 2014). Therefore, without considering the responses of life history traits, functional feeding traits alone failed to evaluate the responses of invertebrates to nutrient changes. Our findings suggested the importance of analysing functional feeding and life history traits together to better illustrate invertebrate trait responses to environmental disturbances (Poff et al., 2006; Verberk et al., 2013; Pilière et al., 2015).

In conclusion, similar responses of functional feeding and life history traits to periphyton biomass and nutrients in our study suggested that evaluating trait responses to nutrients may be sufficient to reflect the effects of nutrient-induced changes in periphyton biomass on stream invertebrates. The responses of shredders more likely reflected nutrient effects acting on food sources, whereas, the responses of algae piercers reflect those on both food sources and habitat changes. Invertebrate traits, therefore, can be used to partition the potential effects of nutrients on food sources and/or habitats of stream invertebrates.

Chapter 5. The effects of nutrient enrichment on the recovery of stream invertebrate communities after large floods

Authors: Yen T.H. Dinh and Russell G. Death

Affiliations: Innovative River Solutions, College of Science, Massey University, Private Bag 11-222, Palmerston North 4442, New Zealand

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Abstract

An increased frequency of 1-in-50-year flood events is a growing threat to lotic ecosystems. However, many watersheds are also adversely affected by high nutrient loads, and it is unclear whether this affects the recovery of stream invertebrates from those floods. We investigated the effects of a 1-in-50-year flood on invertebrate communities at five sites that differed in nutrient levels. Pre-flood samples were collected annually between 2003 and 2015 and post-flood samples were collected five times between May 2015 and March 2016. Invertebrate community responses varied between streams with different nutrient levels and those with and without the forest canopy. In the low nutrient river, the community composition under the forest canopy (S1) recovered by week 9 post-flood due to the high resilience of dominant taxa (*Coloburiscus humeralis* and *Olinga feredayi*); whereas, those in the open canopy (S2) had not recovered by week 40 because of the unrecovered abundance of Oligochaeta. In nutrient-impacted and open-canopied streams (S3-S5), communities dominated by Orthocladiinae and *Potamopyrgus antipodarum* recovered by week 25 post-flood, which may be associated with the regrowth of periphyton. Managers, therefore, need more consideration of open-canopied watersheds at low nutrient levels in the context of future extreme flooding regimes.

Keywords: floods, disturbances, nutrient enrichment, periphyton biomass, stream invertebrates, the presence of a forest canopy.

INTRODUCTION

The frequency of extreme floods (greater than 1-in-50 year events) is predicted to increase in many parts of the world as a result of changes in climate pattern (IPCC, 2013). Invertebrate communities are likely to be more affected by extreme floods than seasonal floods because recovery after extreme floods are likely to take much longer (Lake, 2008; Death et al., 2015; Reich and Lake, 2015). Invertebrate communities took a month to recover after a 1-in-5-year flood (Matthaei et al. 1997) but 3-10 years to recover after a 1-in-50-year flood (Woodward et al., 2015).

Nutrient enrichment, as a result of land-use change, is one of the most prevasive impacts on freshwater ecosystems (Morgan and Cushman, 2005; Strayer and Dudgeon, 2010). Invertebrate richness and abundance, especially for Ephemeroptera, Plecoptera and Trichoptera, commonly decline in nutrient-enriched streams (Morgan and Cushman, 2005; Strayer and Dudgeon, 2010). Eutrophication can result in communities dominated by a few common pollution-tolerant taxa (Olden and Rooney, 2006; Collier, 2008; Piggott et al., 2015).

The dual increases in flood-intensity and nutrient enrichment are likely to become more common (Staudt et al., 2013), however, how these nutrient-enriched ecosystems respond to extreme floods still remains unclear (Death et al., 2015). Pollution-tolerant populations may recover more quickly in nutrient-enriched streams than in low nutrient streams (Vinebrooke et al., 2004; Gafner and Robinson, 2007; Robertson et al., 2015) because of a more rapid recovery of stream periphyton that may facilitate recolonization of invertebrate communities after floods (Biggs, 1995; Death and Zimmermann, 2005; Tonkin et al., 2013). Flow disturbance had no effect on invertebrate communities in streams high in nutrients, whereas, an increase in mayfly abundance and a decrease in chironomid abundance were observed with increased disturbance frequency in low nutrient streams (Gafner and Robinson, 2007). A 1-in-100-year flood in Alaska in 2005 had little effect on the invertebrate communities where chironomids dominated (Robertson et al. 2015). In contrast, recolonization pathways of invertebrate communities, through drift, aerial and within-stream movement, in nutrient-enriched streams might be inhibited because of a greater disconnection within river networks in these highly impacted ecosystems (Death et al., 2015). This may lead to a much longer time for invertebrate communities in nutrient-enriched streams to recover after floods (Staudt et al., 2013).

We are unaware of anyone who has examined the recovery of invertebrate communities after extreme floods in waterbodies that differ in nutrient levels. Heavy rainfall on 14 May, 2015 in the catchments of the Porirua Stream, Horikiri Stream and Waikanae River resulted in the largest flows in these rivers since 1980. This was equivalent to a 1-in-50 year flood event (The Greater Wellington Regional Council, 2015). The streams vary in the degree to which they drain urban or native forest catchments and consequently their degree of human impact and nutrient enrichment. We studied the recovery rate of invertebrate communities at five sampling sites from these three watersheds.

METHODS

Study sites

Two sites on the Waikanae River had the highest water quality: S1, occurred under a dense canopy of native forest, and S2 in open natural grassland. There was one site on the Horikiri Stream that drains predominately agricultural pasture. Two sites on the

Porirua Stream drain an urban and industrial area (Table 1). Nitrate, nitrite, ammoniacal, total nitrogen, dissolved reactive phosphate, and total phosphate concentrations were collected monthly between 2004 and 2015 and analyzed using the standard methods for the examination of water and wastewater (APHA method). The classification of their annual means (using Euclidean distance and group average clustering algorithm) identified three nutrient groups for three watersheds: low (Waikanae River with S1 and S2), medium (Horikiri Stream with S3), and high (Porirua Stream with S4 and S5) (Fig. 1).

Table 1. Characteristics of five study sites. Temperature and conductivity were measured on four post-flood sampling occasions between May and November 2015. Conductivity was standardized at 25°C.

Stream	Site	Easting	Northing	Nutrient level	Canopy cover	Mean temperature (°C)	Mean conductivity (µS/cm)
Waikanae	S1	1779974	5473638	Low	present	9	62
Waikanae	S2	1771223	542915	Low	absent	10	91
Horikiri	S3	1761804	5450653	Medium	absent	12	192
Porirua	S4	1753289	5438364	High	absent	11	229
Porirua	S5	1754366	5443031	High	absent	11	229

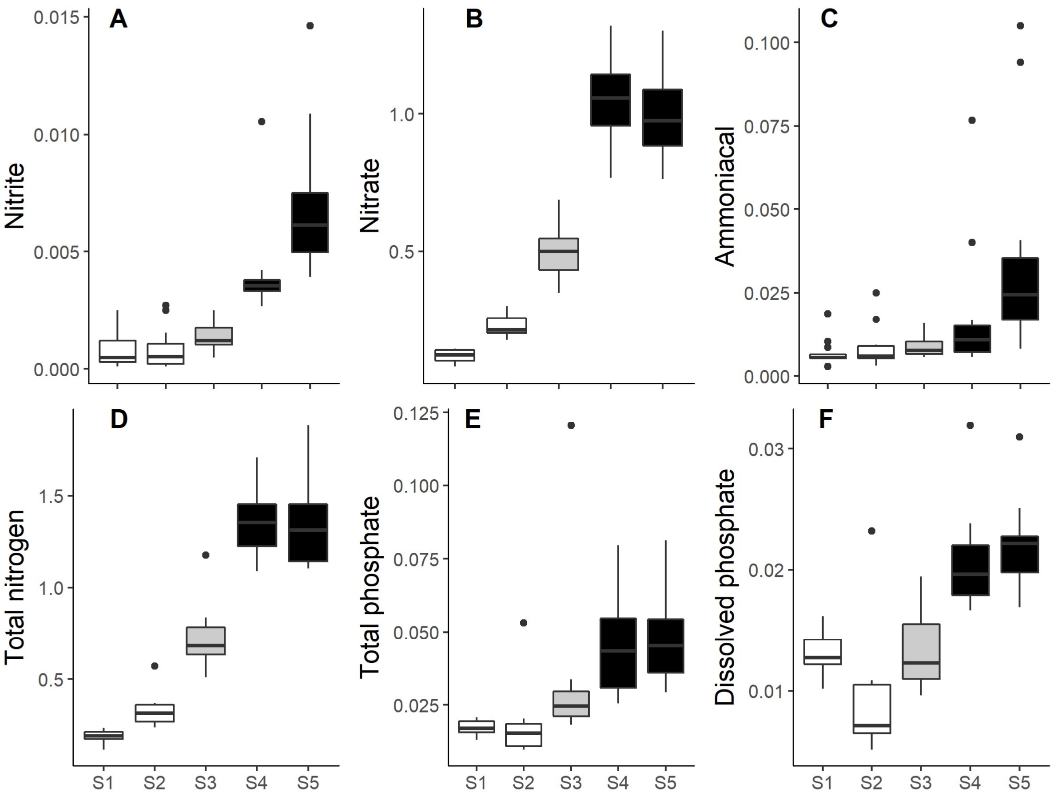

Figure 1. Box-and-whisker plots for nitrite (A), nitrate (B), ammoniacal (C), total nitrogen (D), total phosphate (E) and dissolved reactive phosphate (F) at five sites on the Waikanae River, Horikiri Stream and Porirua Streams in Wellington, New Zealand between 2004 and 2015 before the flood. Low nutrient sites are in white, medium nutrient site in grey, and high nutrient sites in black. Lines in boxes are medians, box ends are quartiles, whiskers are quartiles ± 1.5*IQR (where IQR is the inter-quartile range), and dots are outliers.

Sample collection

We collected samples at the five sites between May and November 2015 on four occasions at 1, 3, 9, and 25 weeks after the flood. Pre-flood data were provided by the Greater Wellington Regional Council (GWRC) who sampled periphyton biomass and invertebrate assemblages annually during late summer/early autumn between 2004 and

2015. Periphyton biomass in 2016 (40 weeks after the flood) was only measured at S3 and S5 (Morar et al., 2016).

GWRC collected periphyton samples by scrubbing a known area from the upper surface of ten randomly chosen rocks and pooling into a single composite sample (Morar et al., 2016). In our study, we collected five stones randomly at each site. All samples were then stored on ice for immediate transport and analysis in the laboratory. The periphyton biomass was measured indirectly by assessing chlorophyll *a* concentration. Pigments were extracted for the GWRC sample by adding 90% boiling ethanol then leaving it at 5°C in the dark for 24 hours (Biggs and Kilroy, 2000). We used a known volume of 90% acetone left at 5°C in the dark for 24 hours (Steinman et al., 2006). Absorbencies of the solution were read using a Varian Cary 50 UV Visible Spectrophotometer for our samples. Samples were converted to pigment concentration following Biggs and Kilroy (2000) or Steinman et al. (2006) for GWRC and our samples, respectively. Pigment concentration in our samples was adjusted by dividing half of the stone surface area (calculated following Graham et al. (1988)) because periphyton is generally found only on the upper exposed surface of stones.

GWRC collected invertebrate samples using semi-quantitative kick samples (or timed kick samples) (Everall et al., 2017). A selected area of substrate (0.1 - 0.2 m^2) was disturbed upstream of the kick net (500 µm mesh size) to direct organisms into the net, and then, repeated in different riffles until a total area of 0.6 -1.0 m^2 was covered within a 50m stream reach. Three replicate kick net samples were collected annually between 2004-2009 but, since 2010, only one kick net was collected (Morar et al., 2016). We collected samples using a Surber sampler. At each site, five 0.1 m^2 Surber samples (250 µm mesh) were collected from riffles by brushing stones and disturbing the substrate. Samples were then stored in 90% propanol and processed in the laboratory. Invertebrates were removed from samples, identified using available keys and counted (Cowley, 1978; Winterbourn et al., 1989; Towns and Peters, 1996). Individuals were identified to the lowest possible taxonomic level, usually genus.

Data analysis

Pre-flood data contained data collected between 2003 and 2015, and post-flood data were those collected on five occasions between May 2015 and March 2016. All analyses were performed in R (version 3.2.4, R Project for Statistical Computing, Vienna, Austria).

We used a non-parametric Kruskal-Wallis test to assess changes in periphyton biomass among sites and between pre- and post-flood data. We then used Mann-Whitney tests to assess differences in biomass between pre- and post-flood at each site. P values were adjusted for multiple test using a Bonferroni correction.

We undertook community composition analyses with the *mvabund* package (version 3.11.4) because the analyses allowed us to examine changes in relative abundance of each taxon rather than its absolute abundance, and therefore the potential effects of sampling difference could be minimized. We used generalized linear model (GLM) in the *manyglm* function to fit relative abundance of each taxon against sites, pre- and post-flood, and their interaction. Characteristic taxa at each site were identified by selecting taxa having p-value ≤ 0.1, in which the p-value of each taxon was obtained by adding *p.uni=adjusted* in the *anova.manyglm* function (Wang et al., 2012). We then performed pairwise comparisons by fitting the abundance of each taxon against pre-and post-flood at each site. The GLMs in the package *mvabund* are adapted for multivariate abundance data because they can be used with strong mean–variance relationships and non-normal data that is often found in ecology (Wang et al., 2012). We tested the significance of each predictor with the *anova.manyglm* function (Wang et al., 2012). The *p*-value was calculated by 999 iterative re-sampling using the probability integral transform residues method (Wang et al., 2012). The *p*-values obtained from pairwise comparisons were adjusted using a Bonferroni correction.

We used a model-based ordination with the *boral* package (version 1.1) (Hui, 2016) to adjust for potential differences in sampling methodology, which common ordination methods such as non-metric multidimensional scaling (nMDS) can not (Warton et al., 2015a; Hui, 2016). The model-based ordination has two parts: the model and the model residuals. The model uses the GLMs to fit abundance of each taxon against environmental variables with the *boral* function. The model residuals represent influences of unfitted variables and can be plotted in a two-dimensional ordination (Warton et al., 2015a; Hui, 2016). The model-based ordination, therefore, allows us to separate effects of each variable from a wide range of measured variables (Warton et al., 2015a; Hui, 2016). As a result, we fixed sampling methods in the main model, therefore, the model residuals were unlikely to be affected by potential differences in sampling methods.

Residuals from the boral function were used to evaluate the recovery rate of community composition after the flood at each site. Site scores on the second latent variable were linked with the flood ($F_{1,83} = 11.65$, $p=0.001$) so we used the first and the third quartile of these pre-flood site scores as a reference state. When a site score of a post-flood replicate at a site was between the first and the third quartiles of pre-flood site scores, it indicated that community composition at the site had recovered by the time the post-flood replicate was collected.

The focus of the study is to study recolonization patterns immediately after the flood. Although it is not ideal to use different sampling techniques, Everall et al. (2017) found no difference between abundant-weighted biomonotring metrics collected by timed kick samples and those collected with Surber samples in UK rivers. Moreover, we also adjusted the potential method effects by using community composition analyses in the *manyglm* (Wang et al., 2012; Warton et al., 2015b) and by fixing sampling methods in the main effects model using the *boral* function (Warton et al., 2015a; Hui, 2016). Consequently, the potential effects of sampling methods is minimized.

RESULTS

The median of pre-flood chlorophyll *a* at S1 was 2.09 mg m^{-2} and, those at S2-S5 ranged from 19.42 to 44.66 mg m^{-2} (Fig. 2). While biomass at S2-S5 did not show a significant difference between pre- and post-flood samples, periphyton biomass at S1 did not recover to the pre-flood level after 40 weeks (Tables 2 & 3).

Pre-flood invertebrate community composition at S1 was significantly different from those at S2-S5 (Table 3 and Fig. 3). Within S2-S5, community composition grouped into low, medium and high nutrient sites (Fig. 3). Community composition was characterized by *O. feredayi* and *C. humeralis* at S1; Orthocladiinae and Oligochaeta at S2, *P. antipodarum* at S3, Orthocladiinae and *P. antipodarum* at S4 and S5 (Fig. 4).

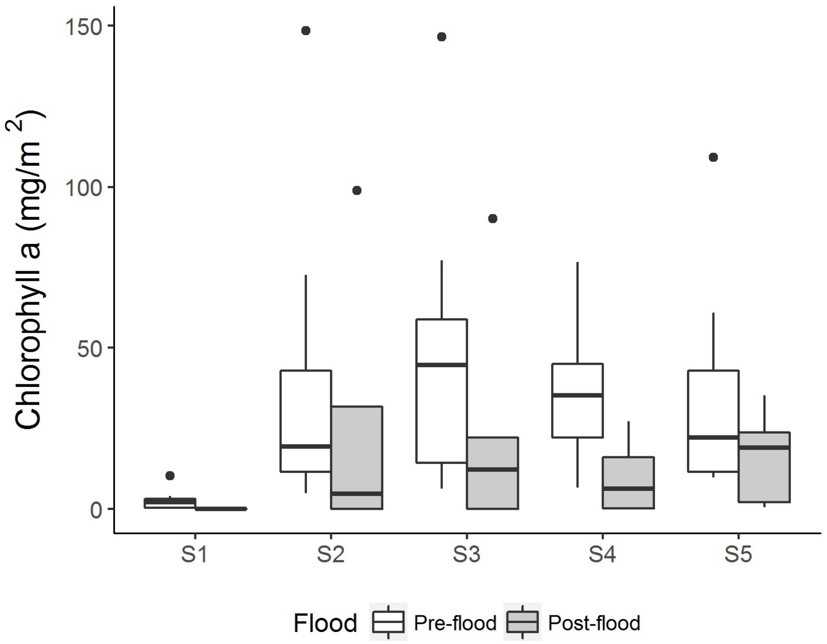

Figure 2. Box-and-whisker plots of periphyton biomass before and after the flood at five sites on the Waikanae River, Horikiri Stream and Porirua Streams in Wellington, New Zealand. Pre-flood biomass is in white and post-flood biomass in grey. Pre-flood samples were collected annually between 2004 and 2015, and post-flood samples were collected five times between May 2015 and February 2016. Lines in boxes are medians, box ends are quartiles, whiskers are quartiles ± 1.5*IQR (where IQR is the inter-quartile range), and dots are outliers.

Table 2. Results of Kruskall-Wallis tests for periphyton and analysis of deviance for invertebrate community composition for differences between sites and pre-and-post-flood. Pre-flood samples were collected annually between 2004 and 2015; and post-flood samples were collected five times between May 2015 and February 2016 at five sites on the Waikanae River, Horikiri Stream and Porirua Stream in Wellington, New Zealand. Df.dff is the degree of freedom; and Dev is the deviance. * = *p< 0.05*, ** = *p< 0.01*.

Model	Periphyton biomass			Community composition		
	df	chi-squared	p	df	Deviance	p
Flood	1	9.9295	0.002**	1	162.4	0.001**
Site	4	24.8	<0.001**	4	1418.5	0.001**
Flood : Site				4	275.4	0.001**

Table 3. Results of post-hoc tests for differences in community compositions between sites at pre-flood. P values obtained from post-hoc tests were adjusted using the Bonferroni correction. Pre-flood samples were collected annually between 2004 and 2015 at five sites on the Waikanae River, Horikiri Stream and Porirua Stream in Wellington, New Zealand.

Paired wise comparisons	p adjusted
S1-S2	0.001
S1-S3	0.001
S1-S4	0.001
S1-S5	0.001
S2-S3	0.001
S2-S4	0.001
S2-S5	0.001
S3-S4	0.001
S4-S5	0.14

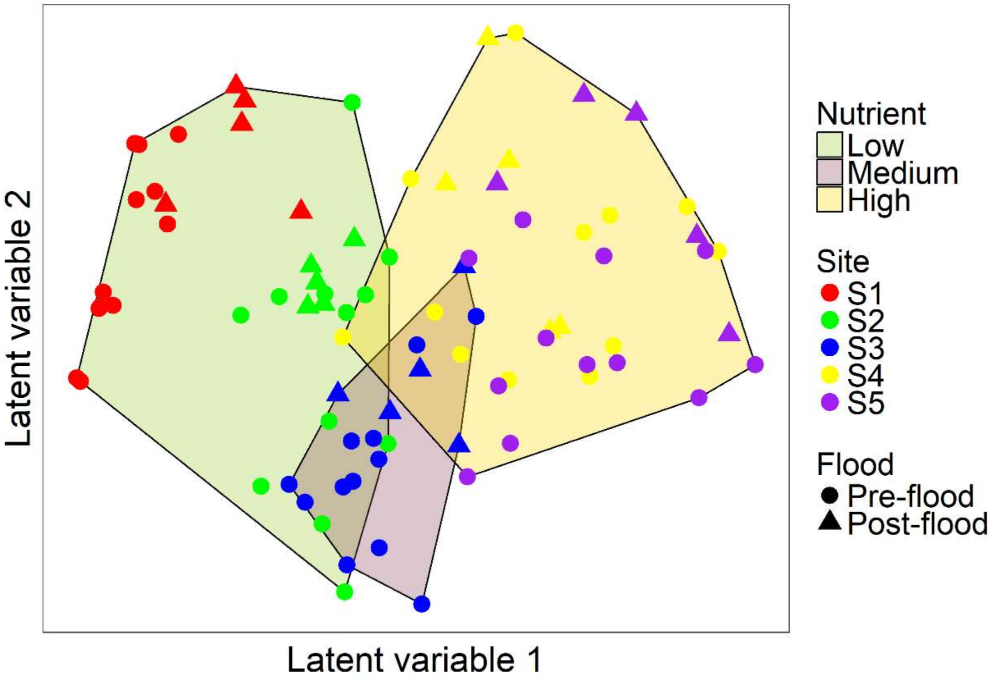

Figure 3. Ordination of community composition at five sites on the Waikanae River, Horikiri Stream and Porirua Streams in Wellington, New Zealand.. Pre-flood samples are in circle and post-flood samples are in square. Pre-flood samples were collected annually between 2004 and 2015, and post-flood samples were collected five times between May 2015 and February 2016.

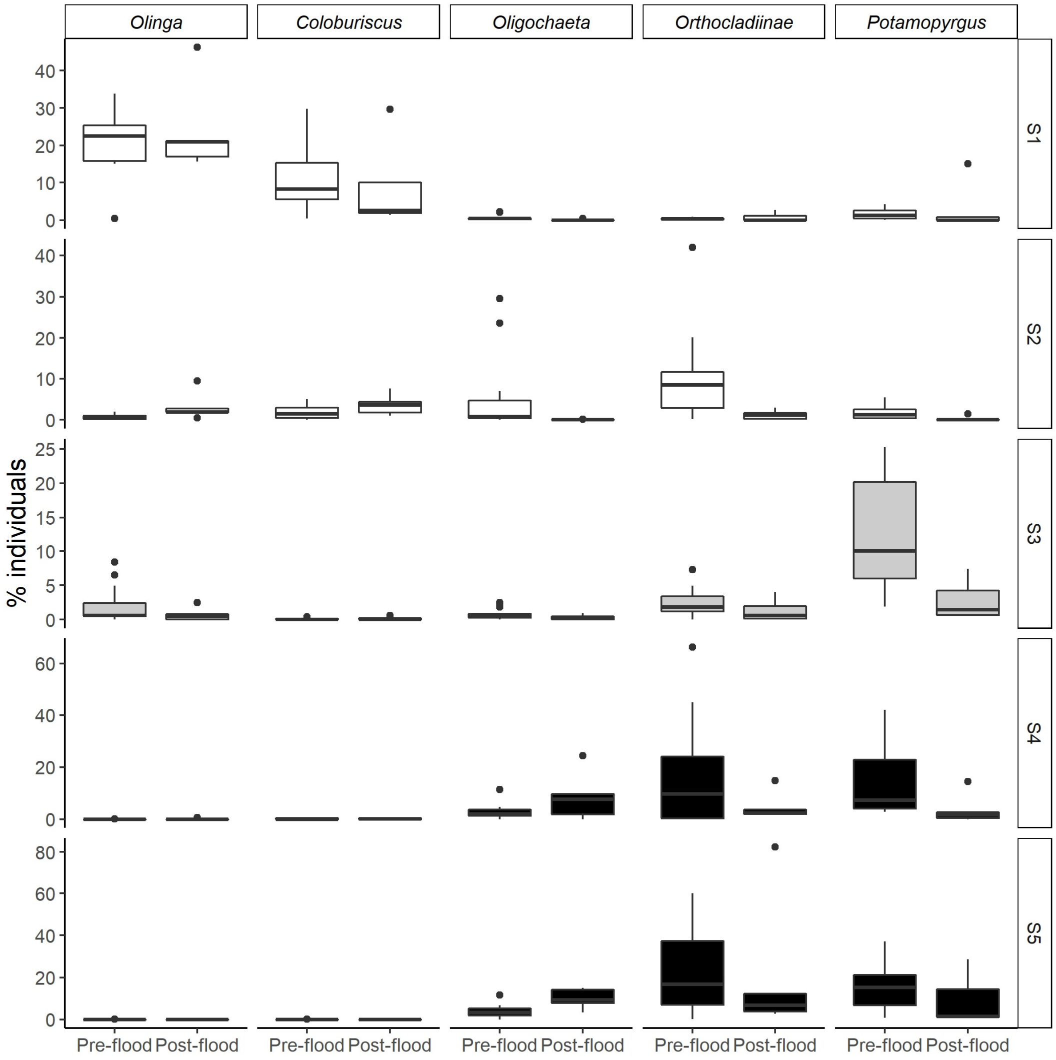

Figure 4. Box-and-whisker plots of percentage of individuals of *Olinga feredayi*, *Coloburiscus humeralis*, Oligochaeta, Orthocladiinae, and *Potamopyrgus antipodarum* before and after the flood at S1 to S5 (from top to bottom). Low nutrient sites are in white, medium nutrient sites in grey, and high nutrient sites in black. Samples were collected on at five sites on the Waikanae River, Horikiri Stream and Porirua Streams in Wellington, New Zealand. Pre-flood samples were collected annually between 2004 and 2015; and post-flood samples were collected five times between May 2015 and February 2016. Lines in boxes are medians, box ends are quartiles, whiskers are quartiles ± 1.5*IQR (where IQR is the inter-quartile range), and dots are outliers.

Community composition at S2 was different after 40 weeks (Table 4) because the post-flood relative abundance of Oligochaeta at S2 was significantly lower than the pre-flood relative abundance (P=0.07) (Fig. 4). In contrast, the site score at S1 by week 9 after the flood was between the first and the third quartiles, whereas, it was week 25 for S3, S4 and S5 (Fig. 5).

Table 4. Results of Mann-Whitney tests (W) for periphyton biomass and analysis of deviance for invertebrate community composition for differences between pre- and post- flood at each site. Pre-flood samples were collected annually between 2004 and 2015; and post-flood samples were collected five times between May 2015 and February 2016 at five sites on the Waikanae River, Horikiri Stream and Porirua Streams in Wellington, New Zealand. '*': significant level <0.05 after Bonferroni correction; 'ns': no significant after Bonferroni correction

Site	Periphyton biomass			Community composition			
	W	p		df	Deviance	p	
S1	2	0.009	*	1	68.63	0.04	ns
S2	13	0.2	ns	1	87.72	0.004	*
S3	17	0.19	ns	1	59.62	0.1	ns
S4	7	0.04	ns	1	55.97	0.16	ns
S5	18	0.23	ns	1	47.76	0.13	ns

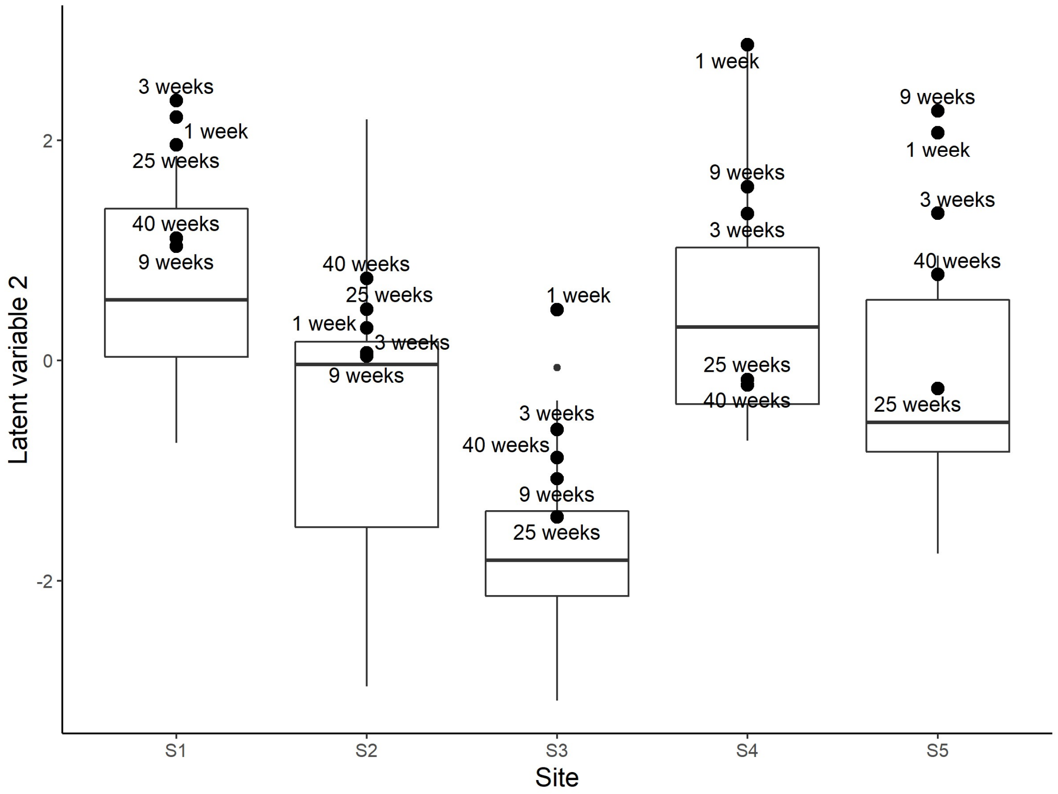

Figure 5. Box-and-whisker plots of pre-flood site scores on the 2nd latent variable at four sites between 2004 and 2015. Post-flood site scores were coded as 1 week, 3 weeks, 9 weeks, 25 weeks, and 40 weeks corresponding for five collected times between May 2015 and February 2016. Samples were taken on the Waikanae River, Horikiri Stream and Porirua Stream in Wellington, New Zealand. Lines in boxes are medians, box ends are quartiles, whiskers are quartiles ± 1.5*IQR (where IQR is the inter-quartile range), and dots are outliers.

DISCUSSION

Invertebrate communities in Waikane River (S1) under the forest canopy recovered by week 9 after the flood because the mayfly *C. humeralis* and the cased caddisfly *O. feredayi*, characteristics of this site, are highly resilient to floods (Jowett et al., 1991). These animals are commonly found in the streams with permanent flow and continuous riparian cover (Jowett et al., 1991; Death, 2003; Tonkin et al., 2013). The mayfly *C. humeralis* have one aquatic stage that reduces the chance of being exposed to destructive flows (Dinh and Death, 2018). The cased caddisfly *O. feredayi* have short-lived adults (less than 10 days) that help them to complete their life cycles quickly and rapidly re-occupy the disturbed habitats when disturbance effects have subsided. These characteristics might explain the high resilience to floods of the mayfly and cased caddisfly (Jowett et al., 1991), leading to the recovery of invertebrate community by week 9 after the flood. Fuller et al. (2008) have also found invertebrate communities at sites under part or full canopy cover are unaffected by floods, whereas, communities in open canopied sites did not recover quickly from floods. Several other studies in New Zealand streams also found that invertebrate communities at sites under forest canopy recovered quickly after floods, while floods reduce periphyton, invertebrate density and diversity in open canopy streams (Death and Zimmermann, 2005; Tonkin et al., 2013). Invertebrate communities in forest streams, therefore, appeared to be highly resilient to large floods.

By week 40 after the flood, the invertebrate community in Waikane River (S2), the low nutrient site in the open canopy, had not recovered, which might be associated with the unrecovered abundance of Oligochaeta. Oligochaeta abundance that feed on fine organic matter were unrecovered at the low nutrient site but recovered at nutrient-enriched sites. Invertebrates recolonize only when their food source recovers (Death and Zimmermann, 2005; Dinh and Death, 2018). Therefore, we propose that the recovery of Oligochaeta abundance at S3-S5 but not S2 may be associated with the level of organic matter input at S3-S5 that drained intensive pasture and urban areas compared to S2 that drained natural grassland.

In contrast, invertebrate communities in nutrient-impacted and open-canopied Horikiri and Porirua Stream (S3-S5) recovered by week 25 after the flood probably because of the recovery of dominant taxa: chironomids Orthocladiinae and the snails *P. antipodarum*. Orthocladiinae are highly resilient to floods (Death, 2008; Robertson et al., 2015). Previous studies have observed a rapid recovery of communities dominated by chironomids after floods (Gafner and Robinson, 2007; Robertson et al., 2015). Midges feed on streambed algae and other fine organic matter, therefore, the regrowth of periphytons might also contribute to the recovery of chironomids at S3-S5. Additionally, more nutrients at S3-S5 resulted in a rapid recovery of periphyton so the grazing snail *P. antipodarum*, who feed on periphyton, can recover quickly. The food base of a community appeared to be important in determining the rate of recovery of these invertebrate communities.

To conclude, the recovery of invertebrate communities after large floods depend on the recovery of the food base of the food web that is, in turn, determined by the presence of a forest canopy cover and nutrient levels in a stream. In the low nutrient Waikanae River, communities under the forest canopy recovered by week 9 after the flood, whereas, those in the open canopy were unrecovered after 40 weeks. This highlights the importance of overhanging vegetation that might have potential to mitigate negative consequences of floods (Death et al., 2015; Dwarakish and Ganasri, 2015). Without the forest canopy, the recovery of invertebrate communities in the nutrient-impacted Horikiri and Porirua Stream, but not those in the low nutrient Waikane River, disagreed with those who stated that ecosystems already severely stressed by human activities are likely to be more sensitive to future flow regimes (Staudt et al., 2013; Death et al., 2015). Future flow regimes with a higher frequency and intensity of large floods will significantly affect invertebrate communities in open-canopied streams with low nutrient levels. Managers, therefore, need to consider those ecosystems to provide better flood management in the context of future flow regimes.

Chapter 6. Does flow disturbance affect diversity and community composition of tropical stream invertebrate communities?

Authors: Yen T. H. Dinh[1], Hieu Van Nguyen[2] and Russell G. Death[1]

Affiliations:

[1] Innovative River Solutions, College of Sciences, Massey University, Private Bag 11-222, Palmerston North, New Zealand

[2] Faculty of Biology - Agricultural Technology, Hanoi Pedagogical University 2, Xuan Hoa, Vinh Phuc, Vietnam

Abstract

Southeast Asian streams are a diversity hot spot, but under an increased risk of dramatic flow changes from land-use and climate change. It is unclear how these hydrological changes might influence diversity and composition of invertebrate communities because little is known about the influence of floods on these communities. Flow disturbance can physically remove animals and periphyton food resources. We investigated the relative contribution of substrate disturbance and periphyton biomass in explaining the diversity and composition of invertebrate communities collected at nine sites in three streams in the Sapa Highland, Vietnam. Elevation appears to have a stronger effect on diversity and species composition than flow disturbance on these invertebrate communities. Species richness, Simpson's diversity index, and community dissimilarity decreased with elevation. Species composition in these streams was also strongly influenced by altitude. The caddisflies *Psilotreta* spp. and coleopterans *Eubrianax* spp. are likely to become endangered in future because they were restricted to high altitude streams.

Keywords: flow disturbance, diversity, food source, tropical streams, invertebrate communities, climate change.

INTRODUCTION

Southeast (SE) Asia is a diversity hot spot, however, this region is facing threats to that diversity from land-use and climate change (Collen et al., 2014). Deforestation rates are at least three times higher in SE Asian forests than in other tropical areas (Sodhi et al., 2010a; Sodhi et al., 2010b; Taniwaki et al., 2017). Deforestation likely results in more frequent short, and unpredictable floods in rivers and streams that in turn have the potential to decrease biodiversity and shift ecosystem function (Taniwaki et al., 2017). Tropical streams are also experiencing changes in the frequency and magnitude of rainfall extremes that are likely unprecedented in the last 5200 years due to climate change (Thompson et al., 2006; IPCC, 2013). Invertebrates in tropical streams are, therefore, under a great risk of extinction (Taniwaki et al., 2017).

Flow disturbances are the principal environmental factor shaping the diversity and community structure in many Mediterranean and temperate streams (Chessman et al., 2010; Dolédec et al., 2017; Tonkin et al., 2017). Hydrological indices explain 41% to 52% of the variation in invertebrate community composition in temperate New Zealand streams (Clausen and Biggs, 1997; Booker et al., 2015). Stream invertebrates are highly sensitive to changes in flow because their specific life-history characteristics are intimately linked with the timing, frequency, and severity of natural flow regimes (Lytle, 2001; Lytle and Poff, 2004). However, we still know little of the effects of flow disturbances on invertebrate communities in tropical streams, especially those in SE Asia (Md-Rawi et al., 2014; Tonkin et al., 2016).

The effect of floods and spates on freshwater animals can be similar, regardless of their geographical location (Lake, 2000; but see Death and Barquín, 2012). Floods increase shear stress on the streambed, causing substrates to move (Neverman et al., 2018). This removes individuals and periphyton, an important food source for many aquatic invertebrates (Scarsbrook and Townsend, 1993; Biggs, 1995; Death and Zimmermann, 2005). Lau et al. (2009) found that periphytic diatoms and cyanobacteria were more important than terrestrial detritus input for tropical streams invertebrates when comparing these two food types in three tropical headwater streams in Hong Kong. Flood disturbance may, therefore, be critical in structuring invertebrate communities of tropical streams. However, it is unclear exactly if flow disturbance structures tropical stream invertebrate communities (Boyero et al., 2009; Md-Rawi et al., 2014; Tonkin et al., 2016). The Sapa Highland is located in the northern region of Vietnam and is one of the biodiversity centres in mainland SE Asia (Jung et al., 2008). We investigated the relative contribution of substrate disturbance and periphyton biomass in determining diversity and community structure of invertebrate communities in these Sapa Highland streams.

METHODS

Study sites and physiochemical measures

Nine sites in three streams in the Sapa Highland were sampled in December 2017. The three streams varied in canopy cover from 0-95%, and drained native forest, forest agriculture and village agriculture (Table 1). The average annual rainfall in the Sapa Highland is 2700 mm, with July and August receiving the highest rainfall. Annual temperature ranges from 3^0C – 20^0C with a yearly average of approximately 15^0C, with December and January being the coldest months.

Temperature, pH, conductivity, and dissolved oxygen were measured at each site using a portable water checker WQX-22A, TOA, Japan. Elevation was measured with a portable global position system (GPS) SP24XC, MLR, USA (Table 1).

Table 1: Physiochemical variables measured at nine sites in three Sapa Highland streams, Vietnam, in December 2017.

Site	Elevation (m)	Pfankuch index	Temperature (^{0}C)	Conductivity (µS/cm)	pH	Dissolved oxygen (mg/l)	Periphyton biomass (µg/cm^2)	Canopy (%)	Landscape
S1	1835.17	22	11.4	9	6.63	10.1	0.095	10-80	Forest
S2	1829.26	23	11.2	6	6.03	10.28	0.12	60-95	Forest
S3	1850.59	29	11.7	12	6.66	9.94	3.42	80-95	Forest
S4	826.29	48	15.3	23	7.42	8.88	0.87	0-20	Village agriculture
S5	685.31	48	18	28	7.6	9.19	0.91	0-5	Village agriculture
S6	622.02	42	16.8	18	7.03	9.21	1.05	0-5	Village agriculture
S7	1596.25	33	13.9	9	6.94	10.28	0.45	0-5	Forest agriculture
S8	1576.095	34	14.5	11	7.21	10.65	1.17	0-5	Forest agriculture
S9	1116.025	40	15.8	50	7.51	9.08	0.13	50-95	Forest agriculture

Substrate disturbance

Substrate disturbance measurement was assessed with the bottom component of the Pfankuch stability index. This has been used in several previous studies of lotic invertebrate communities (Pfankuch, 1975; Winterbourn and Collier, 1987; Death and Winterbourn, 1994a). The bottom component assesses substrates in the wetted portion of the stream channel (e.g. rock shape, brightness, size distribution, packing and any algal or moss cover). The site is qualitatively categorised in one of four classes for each substrate characteristic. Scores are summed to give an overall value ranging from 15 (most stable) to 60 (least stable).

Periphyton biomass

Periphyton biomass was assessed by measuring chlorophyll *a* (Chl *a*) on five randomly collected stones (maximum planar dimension < 60 cm) in riffles at each site. They were kept frozen, and, in the laboratory, pigments were extracted in known volumes of 90% acetone at 5°C in the dark for 24 hours. Absorbencies were read with a Thermo Electron Corporation (CAT 335902) spectrophotometer and converted to pigment concentration following Steinman et al. (2006). The pigment concentration was adjusted by dividing half of the stone surface area (calculated following Graham et al. (1988)) because periphyton is generally found only on the upper exposed surface of stones.

Invertebrate samples

We collected five 0.1 m^2 Surber samples (250 µm mesh) from riffles at each site and stored them in 80% ethanol. In the laboratory, invertebrates were removed from samples, identified to the lowest possible taxonomic level (usually species) based on available keys, and enumerated (Morse et al., 1994; Dudgeon, 1999; Nguyen et al., 2001;

Cao, 2002; Nguyen, 2003; Yule and Sen, 2004; Hoang, 2005; Hoang and Bae, 2006; Chen et al., 2008; Webb and McCafferty, 2008; Nguyen et al., 2012).

Data analysis

Diversity analyses were conducted in the *vegan* package (version 2.4.1) in R (version 3.4.3; R Project for Statistical Computing, Vienna, Austria). Species richness, Simpson's diversity index, rarefied species richness, and abundance were calculated for each replicate.

We performed unconstrained model-based ordination with the *boral* package (version 1.5) (Hui, 2016). The model-based ordination has two parts: the model and the model residuals. When no environmental variable is fitted, the *boral* function fits a pure latent variable model. The model residuals are plotted in a two-dimensional ordination that can be interpreted in the same manner as plots from a non-metric multidimensional scaling (nMDS) (Warton et al., 2015a; Hui, 2016). The generalized linear models in the package *boral* are adapted for multivariate abundance data because they can be used when there is a strong mean–variance relationship and/or non-normal data that are often found in ecology (Wang et al., 2012). The model-based residual ordination has a better efficiency in describing the true relationship between sites than nMDS (Warton et al., 2015a; Hui, 2016). The site effect was fixed to account for the potential effects of replicates. We extracted site scores and species scores for ten species that contributed the most variation in community composition based on the Euclidean norm of their coefficients from the *boral* function.

Species richness, rarefied richness, Simpson's diversity index, abundance, site ordination scores were tested for correlation with conductivity, dissolved oxygen, pH, temperature, and elevation using Pearson's correlation. Diversity metrics and site coordination scores were regressed against substrate disturbance and chlorophyll a separately using the *lm* function in the *stats* package (version 3.4.3). When the relationship between two variables followed a curved line, a quadratic equation was used to fit those variables. All assumptions for the *boral* function and *lm* function were checked and verified.

RESULTS

The Pfankuch index correlated highly with elevation. Both of them correlated with temperature, pH and dissolved oxygen, but not conductivity and chlorophyll a (Table 2).

Table 2. Pearson correlation coefficients between Pfankuch index, chlrophyll a, conductivity, dissolved oxygen, pH, temperature, and elevation measured at nine sites in three Sapa Highland streams, Vietnam, in December 2017. Significant correlations after Bonferroni correction ($p< 0.05$) are in bold.

	Elevation	Pfankuch index	Chla	Conductivity	Dissolved oxygen	pH	Temp
Elevation	1						
Pfankuch index	**-0.93**	1					
Chla	0.12	0.03	1				
Conductivity	-0.59	0.62	-0.18	1			
Dissolved oxygen	**0.84**	**-0.79**	0.05	-0.74	1		
pH	-0.74	**0.87**	-0.03	0.72	-0.62	1	
Temperature	**-0.93**	**0.92**	-0.12	0.63	-0.67	**0.86**	1

Species richness, Rarefied richness and Simpson's index decreased with elevation (Table 3). In contrast, species richness and Simpson diversity index increased with Pfankuch index scores, which explained 55% and 50% of their variation (Table 4 and Fig.

1). Chlorophyll a was correlated with density only, exhibiting a unimodal relationship (Table 4 and Fig. 2).

Table 3. Pearson correlation coefficients between diversity metrics, Boral site ordination scores and conductivity, dissolved oxygen, pH, temperature, and elevation at nine sites in three Sapa Highland streams, Vietnam, in December 2017. Significant correlations (*p*<0.05) are in bold.

	Species richness	Rarefied richness	Simpson index	Density	V1 site scores	V2 site scores
Conductivity	0.02	0.31	0.30	-0.11	0.50	0.26
DO	-0.53	**-0.82**	**-0.82**	-0.10	-0.36	**-0.79**
pH	0.37	0.33	0.34	0.31	**0.93**	0.20
Temperature	0.52	0.40	0.51	0.54	**0.85**	0.39
Elevation	**-0.69**	**-0.68**	**-0.76**	-0.51	**-0.66**	**-0.66**

Table 4. Results from regression of diversity indices and two latent community structure variables with disturbance and periphyton biomass at nine sampling sites in Sapa Highland streams, Vietnam, in December, 2017. The latent variables were obtained from the pure latent model in the *boral* package. * = *p*< 0.05, - = not significant.

	Invertebrate metrics	F (df)	p	adjusted R^2	Relationship shape
Disturbance	Species richness	5.8 (2,6)	0.04*	0.55	Quadratic
	Rarefied richness	4.01 (2,6)	0.08	0.43	Quadratic
	Simpson index	5.04 (2,6)	0.05*	0.5	Quadratic
	Density	2.64 (1,7)	0.15	-	Linear
	V1 site scores	11.61 (1,7)	0.01*	0.57	Linear
	V2 site scores	5.39 (2,6)	0.05*	0.52	Quadratic
Chlorophyll a	Species richness	0.19 (1,7)	0.67	-	Linear
	Rarefied richness	0.14 (1,7)	0.72	-	Linear
	Simpson index	0.008 (1,7)	0.93	-	Linear
	Density	5.73 (2,6)	0.04*	0.54	Quadratic
	V1 site scores	3.53 (2,6)	0.1	-	Quadratic
	V2 site scores	0.09 (1,7)	0.78	-	Linear

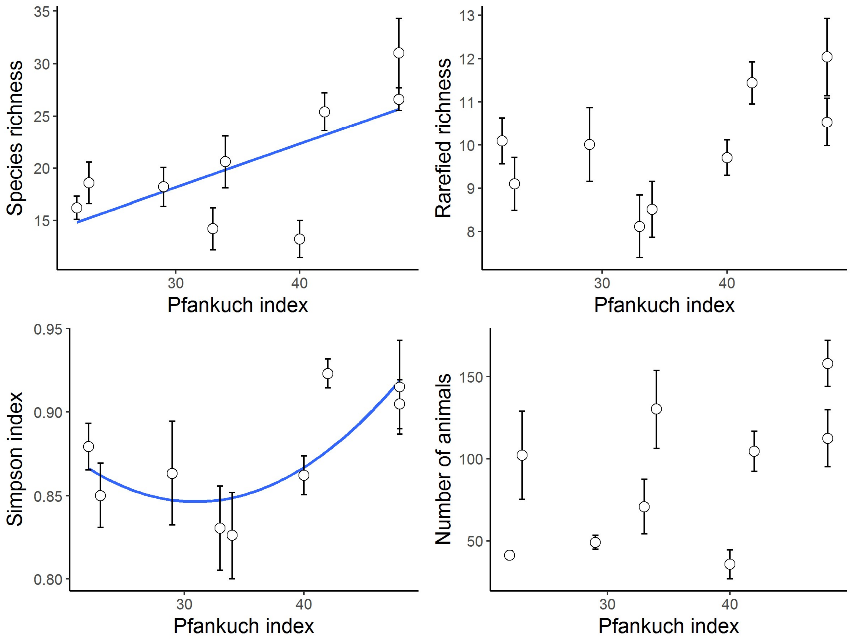

Figure 1. Mean (± SE) Species richness, Rarefied richness, Simpson index and number of animals plotted against Pfankuch index. Samples were collected at nine sites in three Sapa Highland streams, Vietnam, in December 2017.

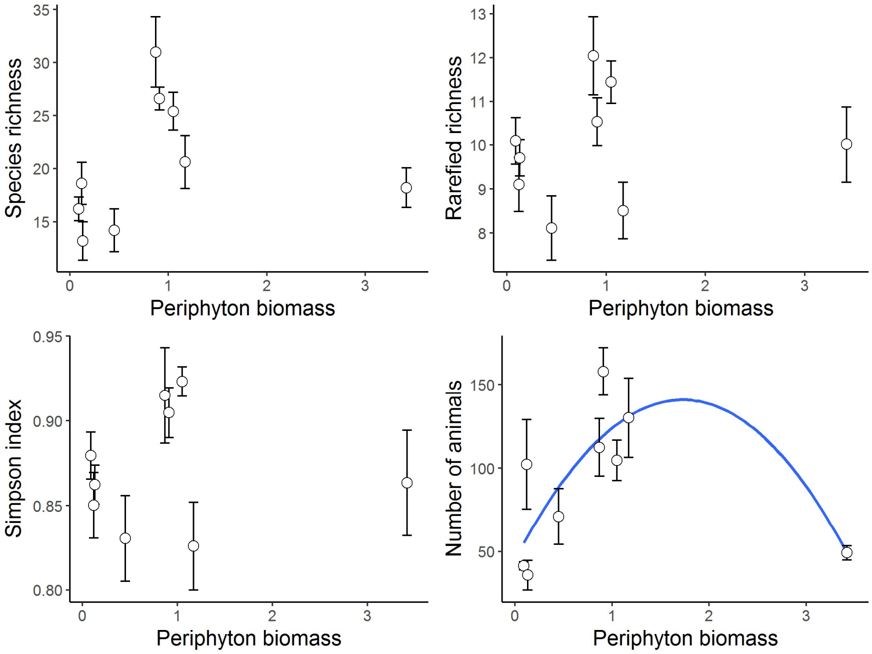

Figure 2. Mean (± SE) Species richness, Rarefied richness, Simpson index and number of animals plotted against periphyton biomass. Samples were collected at nine sites in three Sapa Highland streams, Vietnam, in December 2017.

Boral site ordination scores on both the first and second latent variables were correlated negatively with elevation (Table 3). In contrast, Pfankuch index scores linked positively with these Boral scores, which explained 57% and 52% of their variation in the first and second latent variables (Table 4 and Fig. 3). Chlorophyll did not relate to any of them (Table 4 and Fig. 3).

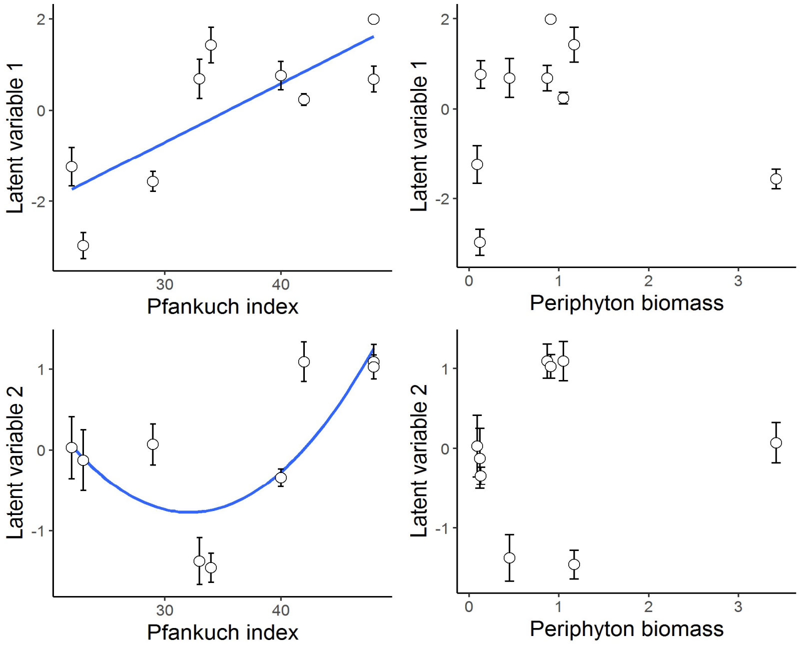

Figure 3. Mean (± SE) site coordination scores on two latent variables plotted against stream disturbance and periphyton biomass. Site coordination scores were obtained from the *boral* function. Samples were collected at nine sites in three Sapa Highland streams, Vietnam, in December 2017.

Abundance of caddisflies *Ceratopsyche* spp., *Cheumatopsche* spp., *Trichomacronema paniae*, and coleopterans *Psephenoides* spp. was positively related Pfankuch index scores, whereas, caddisflies *Psilotreta* spp. and coleopterans *Eubrianax* spp. was negatively associated. Caddisflies *Apsilochorema* spp., mayflies *Epeorus aculeatus*, and dipterans *Tabanus* spp. had peak abundance at an intermediate level of the Pfankuch index (Fig. 4).

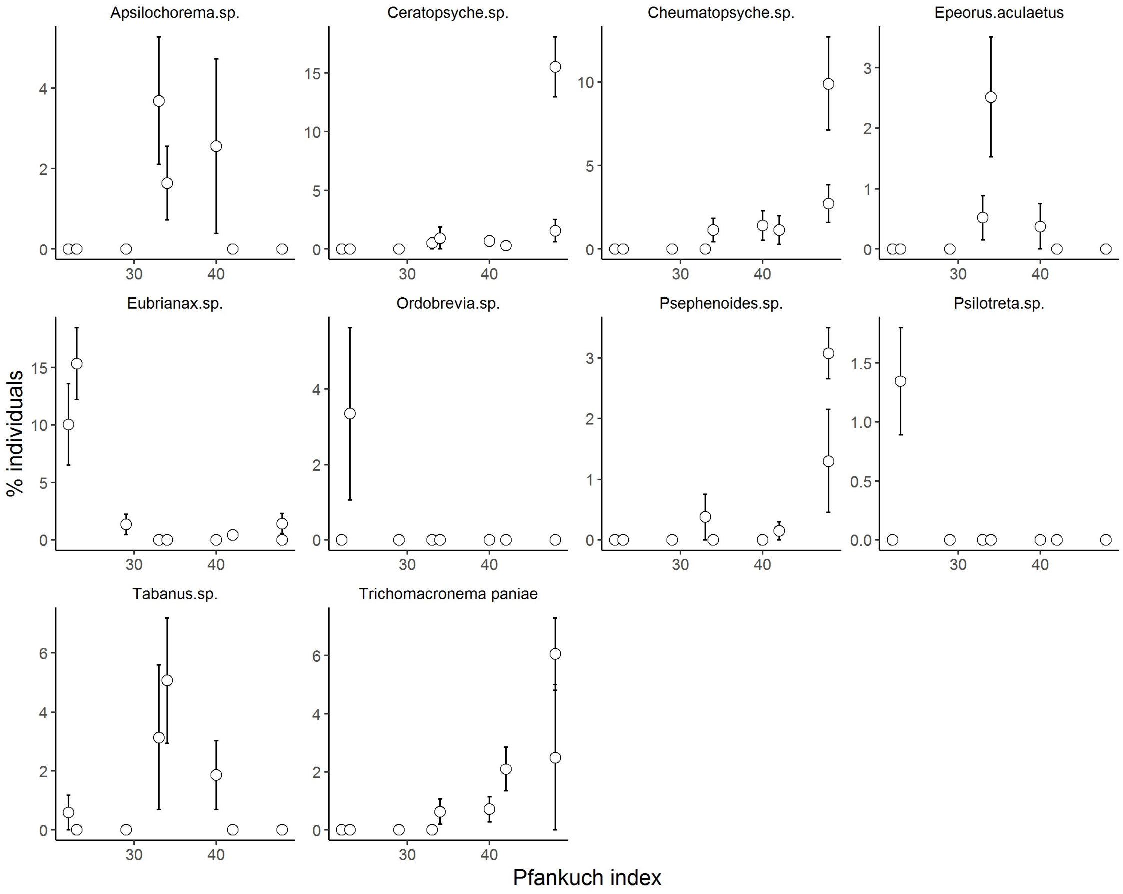

Figure 4. Mean (± SE) ten selected species that contributed the most variation in community composition plotted against stream disturbance. Species scores were obtained from the *boral* function. Samples were collected at nine sites in three Sapa Highland streams, Vietnam, in December 2017.

DISCUSSION

Stream disturbance strongly correlated to elevation, therefore, an increased diversity with disturbance in the Sapa Highland tropical streams might be associated with the high correlation between substrate disturbance and elevation. The positive response of diversity to stream disturbance in our study was inconsistent with studies in temperate streams which recorded either a linear decrease in diversity with disturbance (Death and

Winterbourn, 1995; Tonkin et al., 2013) or peaked at intermediate levels of disturbances (Connell, 1978; Townsend et al., 1997b; Svensson et al., 2007). In contrast, lower diversity at higher altitude is a common pattern in both temperate and tropical regions (Barquín and Death, 2006; Abdo et al., 2013). While non-flying invertebrates cannot travel between catchments, many insects are weak flyers with short-wing and/or a short-lived flying phase, therefore, elevation can be a dispersal barrier for them (Saito et al., 2015; Sarremejane et al., 2017). As a result, the positive response of diversity metrics to stream disturbance might be driven by the negative response of these metrics to elevation.

The lack of association between diversity metrics and periphyton biomass in our study was inconsistent with studies in temperate streams where periphyton biomass set the upper limit to species richness in temperate streams (Death and Winterbourn, 1995; Tonkin et al., 2013). These tropical streams had canopy cover varying from 0-90%, therefore, the low periphyton biomass may relate to the low productivity that might explain an insignificant relationship between diversity metrics and periphyton biomass. Our findings suggest that allochthonnous litter might be a more important food source for invertebrates in tropical streams (but see Lau et al., 2009). However, it remains unclear how these different food sources influence benthic communities because feeding strategies have been little studied in tropical streams (Tomanova et al., 2006; Jung et al., 2008; Boyero et al., 2009).

Density peaked at intermediate levels of periphyton biomass, which has also been found in a number of other temperate stream studies (Huston, 1979; Death and Zimmermann, 2005; Tonkin et al., 2013). However, there was only one site at the high-productivity low-density corner of the spectrum; therefore, we cannot conclude whether or not the association between density and periphyton biomass in these tropical streams conforms to the unimodal relationship as observed in temperate streams (Huston, 1979;

Death and Zimmermann, 2005; Tonkin et al., 2013). Further studies are needed to identify the unimodal of the association between density and periphyton biomass.

The relationship between disturbance and periphyton has been intensively studied in temperate streams, however, to our knowledge; this study is the first one assessing those potential effects on invertebrate diversity and community compositions in tropical streams. Studies in temperate streams have found either additive or multiplicative interactions occurring between periphyton biomass and disturbance (Cardinale et al., 2006; Tonkin et al., 2013; Dinh and Death, 2018). In contrast to these temperate studies, the effects of elevation overrode those of substrate disturbance on diversity metrics and species composition of invertebrate communities in these tropical streams (but see Death and Barquín (2012)); whereas, periphyton biomass did not link with any of them. Therefore, altitude rather than flow disturbance affected diversity and species compositions of invertebrate communities in the Sapa Highland tropical streams. Saito et al. (2015) found that dispersal distance was more important than environmental dissimilarity in explaining phylogenetic beta diversity of insect communities in headwater streams in south-eastern Brazil. In contrast, Smith et al. (2015) found a stronger influence of environmental dissimilarity in Chesapeake Bay in USA. Therefore, the relative importance between altitude and habitat characteristics is likely to depend on the context of the study (Curry and Baird, 2015). Whether or not that altitude is more important than disturbance regime in determining invertebrate diversity and communities in tropical streams may require further studies.

Species composition in these tropical streams was strongly influenced by altitude, in which caddisflies *Ceratopsyche* spp., *Cheumatopsche* spp., *Trichomacronema paniae*, and coleopterans *Psephenoides* spp. found in the low elevation streams (higher disturbance), caddisflies *Psilotreta* spp. and coleopterans *Eubrianax* spp. found in the high elevation streams (lower disturbance); and caddisflies *Apsilochorema* spp., mayflies *Epeorus aculeatus*, and dipterans *Tabanus* spp. found in the intermediate elevation streams (intermediate disturbance). Climate change will likely have stronger negative effects on species that are restricted in high altitude streams (Conti et al., 2014), therefore, caddisflies *Psilotreta* spp. and coleopterans *Eubrianax* spp. will be potentially endangered in the future climate.

Chapter 7. Synthesis

The aim of this thesis was to evaluate the effects of hydrological and nutrient disturbance on invertebrate communities in streams predominately with a trait-based approach. In order to accomplish this, I studied invertebrate communities in UK, New Zealand and Vietnamese streams, and applied fourth corner models, Bayesian ordination, and regression.

Effects of hydrological disturbances

In temperate streams, invertebrates have traits that are highly adapted to flow conditions of their habitats. NZ mountain streams with greater substrate disturbance increased the abundance of plastron-respires, but not those having two aquatic life stages or who were filter feeders. UK rivers with predictable multiple high flows per year supported individuals having highly synchronized life history strategy; rivers with one prolonged rising climb and strong groundwater influence were better for those having a high reproduction strategy, and rivers with a steep peak flow supported both strategies. Therefore, any flow alteration can cause severe consequences to invertebrate communities if local invertebrate traits are not compatible to new flow conditions.

In contrast to these temperate studies, elevation was more important than substrate disturbance in determining diversity and community composition in the Vietnamese streams sampled. Further studies in tropical streams are needed to clarify the role elevation and disturbance regime play in determining invertebrate diversity and community structure.

Effects of nutrient

Nutrients affect functional feeding and life history traits via promoting algal overgrowth in NZ streams. Both periphyton biomass and nutrients increased the abundance of algae piercers but decreased the abundance of shredders. Abundance of collectors being plurivoltine increased with periphyton biomass and nutrients; whereas, those being univoltine decreased their abundance. Scrapers having one aquatic life stages and sexual reproduction decreased abundance with high periphyton biomass and nutrients while those having two aquatic life stages and hermaphroditic ability increased. Therefore, it is important to assess changes in both functional feeding and life history traits of invertebrates to adequately evaluate the effects of nutrients on stream communities.

Combined effects of flow and nutrient disturbances

The recovery of macro-invertebrate communities after floods depended on the recovery of the food base of the food web that was, in turn, determined by the presence of a forest canopy cover and nutrient levels in a stream (Chapter 5). Invertebrate communities under the forest canopy and those in nutrient-enriched streams were more resilient to large floods than communities in the open canopy streams with low nutrient level. The principal driver of flow disturbance on invertebrate traits in the New Zealand light-limiting streams was the physical removal via substrate disturbance. After a 1-in-50-year flood in Wellington, New Zealand, invertebrate communities within the forest canopy stream recovered by week 9 after the flood because their dominant taxa, which were *Olinga feredayi* and *Coloburiscus humeralis*, have highly resilient/resistant traits to high flows. Invertebrates having short-lived adults and univoltine, which are characteristics of *Olinga feredayi,* can complete their life cycles quickly and re-occupy the disturbed habitats while those having one aquatic stage, which is characteristic of *Coloburiscus humeralis,* can limit the change to be exposed to flow disturbances during their time inside the streams. In New Zealand open-canopied streams, invertebrates recolonize after disturbances only when their food sources recover. Nutrients increased midge Orthocladiinae and the snail *Potamopyrgus antipodarum*, which feed on periphyton biofilm, in Wellington nutrient-enriched streams. A rapid recovery of periphyton biomass resulted in the recovery of midges Orthocladiinae and the snails *P. antipodarum* in these nutrient-enriched streams, leading to the recovery of these invertebrate communities by week 25 after the 1-in-50-year flood. In contrast, invertebrate communities in low nutrient stream unrecovered by week 40 probably because Oligochaeta abundance had not recovered, which might be associated with the recovery of their food source, organic matter input, after the flood.

A trait-based approach better explains mechanistic linkages between taxa and environment

Studying invertebrate traits better explains the pattern of invertebrate abundances along the environmental gradient thanks to mechanistic linkages between trait-environment associations, which a taxonomic-based approach does not have. Firstly, flow disturbance can physically remove animals and periphyton; however, it has no or little effect on invertebrate communities in taxonomic-based studies (Scarsbrook and Townsend, 1993; Death and Zimmermann, 2005; Tonkin et al., 2013). The strong influence of substrate disturbance and periphyton biomass on trait composition of stream invertebrate communities in Chapter 2 may explain the high resilience of these communities to flow disturbance that was observed by Death and Zimmermann (2005) in their taxonomically focused study. Secondly, nutrients affect invertebrates through changes in food sources and habitats via promoting epilithon to overgrow the substrate (Matthaei et al., 2010; Wagenhoff et al., 2012; Lange et al., 2014). The responses of shredders likely reflected nutrient effects on periphyton, whereas, the responses of algae piercers reflected both food source and habitat changes. Invertebrate traits can be used to partition the potential effects of nutrients on food sources and/or habitats of invertebrates, which taxonomic-based studies could not. Consequently, trait-based approaches provide insight into how invertebrates respond to disturbances, and can increase understanding of actual mechanistic links. These findings highlighted the importance of examining both taxonomic and functional responses to advance our understanding of the environmental drivers of community composition and maybe broader ecological questions.

Proposed solutions for two limitations of the current trait-based studies

Two limitations of the current trait-based studies are (i) that does not account linkages and interaction among traits, especially life history traits that are evolutionarily auto-correlated, and/or (ii) that cannot analyse abundance data, multiple traits and multiple environmental variables at a time (Dolédec et al., 1996; Legendre et al., 1997; Poff et al., 2006; Menezes et al., 2010; Verberk et al., 2013). The life history strategy approach that accounts for trait linkages and interactions (Poff et al., 2006; Verberk et al., 2013) improved the power to link traits with flow regimes in UK and Wales rivers. Additionally, fourth corner models allow users to integrate abundance data, multiple traits, and multiple environmental variables at a time (Brown et al., 2014; Warton et al., 2015b). Trait combinations of each taxon are reserved and linked in models, therefore, results from fourth-corner models may also have the potential to account for trait linkages. Fourth corner models better clarified how hydrological and nutrient disturbance affect invertebrate communities in New Zealand streams. Therefore, the life history approach and fourth corner models provide great potential solutions for the two limitations of the current trait-based studies.

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APPENDIX A: Statement of author contribution

DRC 16

MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Yen Thi Hai Dinh

Name/Title of Principal Supervisor: Prof Russell Death

Name of Published Research Output and full reference:

Dinh YTH, Death RG. 2018. Do disturbance and periphyton productivity affect stream invertebrate traits? Freshwater Science. 37(2): 367-379.

In which Chapter is the Published Work: 2

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:
  and / or
- Describe the contribution that the candidate has made to the Published Work:
  Yen TH Dinh reviewed literature, carried out the analysis, interpreted the data, wrote the manuscript. Professor Russell Death provided guidance on conception, manuscript development and editing.

Date 27th July 2018

Candidate's Signature

Date: 27th July 2018

Principal Supervisor's signature

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We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Yen Thi Hai Dinh

Name/Title of Principal Supervisor: Prof Russell Death

Name of Published Research Output and full reference:

The effects of flow regime on life history strategies of aquatic macroinvertebrate communities.

In which Chapter is the Published Work: 3

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:
  and / or
- Describe the contribution that the candidate has made to the Published Work:

Yen TH Dinh reviewed literature, carried out the analysis, interpreted the data, wrote the manuscript. Professor Russell Death provided guidance on conception, manuscript development and editing.

Date 27th July 2018

Candidate's Signature

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Principal Supervisor's signature

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Name of Candidate: Yen Thi Hai Dinh

Name/Title of Principal Supervisor: Prof Russell Death

Name of Published Research Output and full reference:

The effects of nutrient enrichment on invertebrate traits in New Zealand streams.

In which Chapter is the Published Work: 4

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate: and / or
- Describe the contribution that the candidate has made to the Published Work: Yen TH Dinh reviewed literature, carried out the analysis, interpreted the data, wrote the manuscript. Professor Russell Death provided guidance on conception, manuscript development and editing.

Date 27th July 2018

Candidate's Signature

Date: 27th July 2018

Principal Supervisor's signature

DRC 16

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We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: **Yen Thi Hai Dinh**

Name/Title of Principal Supervisor: **Prof Russell Death**

Name of Published Research Output and full reference:

The effects of nutrient enrichment on the recovery of stream macroinvertebrate communities after large floods.

In which Chapter is the Published Work: **5**

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:
  and / or
- Describe the contribution that the candidate has made to the Published Work:
  Yen TH Dinh reviewed literature, took post-flood samples, carried out the analysis, interpreted the data, wrote the manuscript. Professor Russell Death provided guidance on conception, manuscript development and editing.

Date 27th July 2018

Candidate's Signature

Date: 27th July 2018

Principal Supervisor's signature

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STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Yen Thi Hai Dinh

Name/Title of Principal Supervisor: Prof Russell Death

Name of Published Research Output and full reference:

Does flow disturbance affect diversity and community composition of tropical stream invertebrate communities?

In which Chapter is the Published Work: 6

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate: and / or
- Describe the contribution that the candidate has made to the Published Work: Yen TH Dinh reviewed literature, collected samples, carried out the analysis, interpreted the data, wrote the manuscript. Professor Russell Death provided guidance on conception, manuscript development and editing.

Date 27th July 2018

Candidate's Signature

Date: 27th July 2018

Principal Supervisor's signature

Appendix B. List of families and their life history strategy in Chapter 3. Trait information and strategies were obtained from Tachet et al. (2010), Verberk et al. (2008a), Poff et al. (2006), and Vieira et al. (2006).

Phylum/Order	Taxa	Life history
Hygrophila	Acroloxidae	S4
Odonata	Aeshnidae	D1
Araneae	Agelinidae	T1
Basommatophora	Ancylidae	S4
Hemiptera	Aphelocheiridae	S2
Isopoda	Asellidae	R3
Decapoda	Astacidae	R3
Ephemeroptera	Baetidae	D3
Tricoptera	Beraeidae	S1
Littorinimorpha	Bithyniidae	S4
Tricoptera	Brachycentridae	S1
Ephemeroptera	Caenidae	S1
Odonata	Calopterygidae	D2
Plecoptera	Capniidae	S1
Diptera	Ceratopogonidae	T1
Diptera	Chaoboridae	T1
Diptera	Chironomidae	T1
Diptera	Chironomini	T1
Plecoptera	Chloroperlidae	S1
Coleoptera	Chrysomelidae	D1
Cladocera	Cladocera	R3
Odonata	Coenagrionidae	D2
Collembola	Collembola	R3
Copepoda	Copepoda	R3
Hemiptera	Corixidae	D1
Amphipods	Corophiidae	R3
Amphipods	Crangonyctidae	R3
Plumatellida	Cristatellidae	S4
Diptera	Culicidae	D1

Cladocera	Daphniidae	R3
Tricladida	Dendrocoelidae	R2
Diptera	Diamesinae	T1
Diptera	Diptera	D3
Diptera	Dixidae	S1
Tricladida	Dugesiidae	S4
Coleoptera	Dytiscidae	D1
Coleoptera	Elmidae	R1
Diptera	Empididae	S1
Ephemeroptera	Ephemerellidae	S1
Ephemeroptera	Ephemeridae	D3
Diptera	Ephydridae	D3
Copepoda	Ergasilidae	R3
Arhynchobdellida	Erpobdellidae	R2
Amphipods	Gammaridae	R3
Hemiptera	Gerridae	S2
Rhynchobdellida	Glossiphoniidae	S4
Haplotaxida	Glossoscolecidae	S4
Tricoptera	Glossosomatidae	S1
Tricoptera	Goeridae	S1
Odonata	Gomphidae	D2
Gordioidea	Gordiidae	R3
Coleoptera	Gyrinidae	D1
Coleoptera	Haliplidae	D1
Haplotaxida	Haplotaxidae	S4
Ephemeroptera	Heptageniidae	S1
Arhynchobdellida	Hirudinidae	S4
Trombidiformes	Hydracarina	T1
Coleoptera	Hydraenidae	D1
Anthoathecata	Hydridae	T2
Littorinimorpha	Hydrobiidae	R3
Hemiptera	Hydrometridae	R1
Coleoptera	Hydrophilidae	D1
Tricoptera	Hydropsychidae	D2
Tricoptera	Hydroptilidae	S1

Coleoptera	Hygrobiidae	D1
Tricoptera	Lepidostomatidae	S1
Tricoptera	Leptoceridae	S1
Ephemeroptera	Leptophlebiidae	D3
Odonata	Lestidae	S1
Plecoptera	Leuctridae	S1
Tricoptera	Limnephilidae	S1
Diptera	Limoniinae	T1
Haplotaxida	Lumbricidae	T2
Lumbriculida	Lumbriculidae	S4
Basommatophora	Lymnaeidae	S4
Tricoptera	Molannidae	S1
Diptera	Muscidae	T1
Haplotaxida	Naididae	R4
Nematoda	Nematoda	R3
Nematomorpha	Nematomorpha	R3
Plecoptera	Nemouridae	S1
Hemiptera	Nepidae	R1
Cycloneritida	Neritidae	S4
Hemiptera	Notonectidae	D1
Tricoptera	Odontoceridae	S1
Oligochaete	Oligochaeta	T2
Diptera	Orthocladiinae	T1
Ostracoda	Ostracoda	R3
Plecoptera	Perlidae	D3
Plecoptera	Perlodidae	S1
Tricoptera	Philopotamidae	S1
Tricoptera	Phryganeidae	D2
Basommatophora	Physidae	S4
Rhynchobdellida	Piscicolidae	S4
Tricladida	Planariidae	R2
Basommatophora	Planorbidae	S4
Odonata	Platycnemididae	D2
Hemiptera	Pleidae	D1
Tricoptera	Polycentropodidae	S1

Porifera	Porifera	T2
Diptera	Prodiamesinae	S1
Diptera	Psychodidae	T1
Tricoptera	Psychomyiidae	S1
Diptera	Ptychopteridae	T1
Lepidoptera	Pyralidae	S1
Diptera	Rhagionidae	T1
Tricoptera	Rhyacophilidae	S1
Coleoptera	Scirtidae	D1
Tricoptera	Sericostomatidae	S1
Megaloptera	Sialidae	T1
Diptera	Simuliidae	D2
Neuroptera	Sisyridae	S2
Veneroida	Sphaeriidae	R3
Haplosclerida	Spongillidae	T2
Diptera	Stratiomyidae	D2
Stylommatophora	Succineidae	R3
Diptera	Tabanidae	D2
Plecoptera	Taeniopterygidae	S1
Diptera	Tanypodinae	T1
Diptera	Tanytarsini	T1
Diptera	Tipulidae	T1
Diptera	Tipulinae	T1
Haplotaxids	Tubificidae	R4
Unionoida	Unionidae	R3
Heterostropha	Valvatidae	S4
Hemiptera	Veliidae	S2
Stylommatophora	Vertiginidae	S4
Architaenioglossa	Viviparidae	S4
Stylommatophora	Zonitidae	S4

Appendix C. Raw invertebrate data

Table C1. Raw relative abundance of invertebrate data collected at five sites from three streams in Wellington, New Zealand (Chapter 5) between 2004 and 2016. Values are sum number of individuals collected at each site.

Site	Flood	Year	*Acanthophlebia*	Acari	*Ameletopsis*	Amphipoda	*Aoteapsyche*	*Aphrophila*	*Archichauliodes*	*Austroclima*	*Austroperla*	*Austrosimulium*
S1	Pre-flood	2004	5	0	4	0	53	0	8	0	3	3
S1	Pre-flood	2005	25	0	3	0	485	30	47	10	35	0
S1	Pre-flood	2006	67	20	27	0	1293	60	100	27	107	0
S1	Pre-flood	2007	128	0	0	0	731	53	117	37	32	27
S1	Pre-flood	2008	85	0	5	0	501	27	107	0	37	0
S1	Pre-flood	2009	67	21	16	0	320	0	149	0	59	24
S1	Pre-flood	2010	16	0	0	0	48	0	16	0	48	0
S1	Pre-flood	2011	32	0	32	0	512	0	64	0	32	0
S1	Pre-flood	2012	11	0	0	0	53	0	32	0	32	0
S1	Pre-flood	2013	48	0	12	0	76	4	28	0	12	0
S1	Pre-flood	2014	0	0	0	0	32	0	16	0	32	16
S1	Pre-flood	2015	48	0	0	0	0	0	32	0	16	0
S1	Post-flood	2015_2	0	0	0	0	6	0	1	0	3	0
S1	Post-flood	2015_3	0	0	0	0	0	0	0	0	3	0
S1	Post-flood	2015_4	0	0	0	0	2	0	1	0	1	0
S1	Post-flood	2015_5	0	1	1	0	1	0	1	0	2	0
S1	Post-flood	2016	8	0	0	0	64	0	8	0	0	0
S2	Pre-flood	2004	0	0	0	0	2	0	1	0	2	6
S2	Pre-flood	2005	0	0	0	0	57	4	4	0	9	22
S2	Pre-flood	2006	0	0	0	0	755	5	13	36	0	0
S2	Pre-flood	2007	0	0	0	0	2075	32	53	101	0	11
S2	Pre-flood	2008	0	0	0	0	472	48	24	120	0	0
S2	Pre-flood	2009	0	0	0	0	97	5	15	0	0	9
S2	Pre-flood	2010	0	0	0	0	32	0	8	48	0	0
S2	Pre-flood	2011	0	0	0	0	5232	16	48	112	0	272
S2	Pre-flood	2012	0	0	0	32	629	11	21	117	0	0
S2	Pre-flood	2013	0	0	0	0	264	24	0	8	0	0
S2	Pre-flood	2014	0	11	0	0	245	21	0	0	0	11
S2	Pre-flood	2015	0	6	0	0	38	32	0	6	0	0
S2	Post-flood	2015_2	0	0	0	1	32	3	1	0	3	2
S2	Post-flood	2015_3	0	0	0	0	54	0	3	0	1	0
S2	Post-flood	2015_4	0	0	0	0	34	1	3	0	0	0
S2	Post-flood	2015_5	0	0	0	0	5	16	2	0	0	1

Site	Flood	Year	*Acanthophlebia*	Acari	*Ameletopsis*	Amphipoda	*Aoteapsyche*	*Aphrophila*	*Archichauliodes*	*Austroclima*	*Austroperla*	*Austrosimulium*
S2	Post-flood	2016	0	0	0	0	56	8	8	0	0	8
S3	Pre-flood	2004	0	0	0	0	29	0	64	181	0	84
S3	Pre-flood	2005	0	0	0	0	105	0	441	273	0	3
S3	Pre-flood	2006	0	0	0	0	1747	0	327	2567	0	167
S3	Pre-flood	2007	0	0	0	0	3445	11	544	2544	0	16
S3	Pre-flood	2008	0	0	0	0	333	0	235	623	0	0
S3	Pre-flood	2009	0	0	0	0	1312	0	128	176	0	152
S3	Pre-flood	2010	0	0	0	0	944	16	64	336	0	0
S3	Pre-flood	2011	0	16	0	0	16	16	16	16	0	0
S3	Pre-flood	2012	0	0	0	0	896	48	48	176	0	16
S3	Pre-flood	2013	0	0	0	32	480	224	128	576	0	64
S3	Pre-flood	2014	0	64	0	0	608	96	96	192	0	0
S3	Pre-flood	2015	0	8	0	0	176	56	8	12	0	0
S3	Post-flood	2015_2	0	0	0	1	38	0	8	0	0	0
S3	Post-flood	2015_3	0	0	0	1	71	0	11	0	0	2
S3	Post-flood	2015_4	0	0	0	1	78	33	2	0	0	4
S3	Post-flood	2015_5	0	0	0	1	38	134	17	0	0	4
S3	Post-flood	2016	0	0	0	0	168	200	96	200	0	0
S4	Pre-flood	2004	0	0	0	1	0	0	4	1	0	1
S4	Pre-flood	2005	0	0	0	0	55	0	22	0	4	0
S4	Pre-flood	2006	0	0	0	0	242	62	139	0	0	20
S4	Pre-flood	2007	0	16	0	0	296	0	104	104	0	0
S4	Pre-flood	2008	0	0	0	0	296	67	317	8	0	21
S4	Pre-flood	2009	0	0	0	3	635	0	200	19	16	51
S4	Pre-flood	2010	0	11	0	0	533	11	53	11	0	0
S4	Pre-flood	2011	0	0	0	0	5	11	96	0	0	5
S4	Pre-flood	2012	0	0	0	0	96	0	171	0	0	11
S4	Pre-flood	2013	0	0	0	16	224	48	32	0	0	0
S4	Pre-flood	2014	0	0	0	0	128	0	64	0	0	128
S4	Pre-flood	2015	0	16	0	0	16	0	32	0	0	48
S4	Post-flood	2015_2	0	0	0	1	1	0	5	0	0	0
S4	Post-flood	2015_3	0	0	0	2	17	0	10	0	1	1
S4	Post-flood	2015_4	0	0	0	0	5	6	9	0	0	0
S4	Post-flood	2015_5	0	0	0	0	4	3	14	0	0	2
S4	Post-flood	2016	0	16	0	0	160	64	48	0	0	16
S5	Pre-flood	2004	0	9	0	10	9	0	0	5	0	40

Site	Flood	Year	*Acanthophlebia*	Acari	*Ameletopsis*	Amphipoda	*Aoteapsyche*	*Aphrophila*	*Archichauliodes*	*Austroclima*	*Austroperla*	*Austrosimulium*
S5	Pre-flood	2005	0	0	0	0	374	4	18	0	0	0
S5	Pre-flood	2006	0	0	0	0	503	7	40	12	0	10
S5	Pre-flood	2007	0	0	0	0	4336	0	56	64	0	40
S5	Pre-flood	2008	0	0	0	5	14	3	23	11	0	0
S5	Pre-flood	2009	0	0	0	0	360	0	112	152	0	8
S5	Pre-flood	2010	0	16	0	0	1312	0	16	32	0	0
S5	Pre-flood	2011	0	0	0	0	518	0	6	0	0	6
S5	Pre-flood	2012	0	0	0	0	72	24	48	32	0	16
S5	Pre-flood	2013	0	80	0	32	32	16	80	0	0	0
S5	Pre-flood	2014	0	0	0	0	2112	32	128	0	0	0
S5	Pre-flood	2015	0	32	0	0	192	0	256	0	0	32
S5	Post-flood	2015_2	0	0	0	5	1	2	1	0	0	0
S5	Post-flood	2015_3	0	0	0	3	6	0	8	0	0	0
S5	Post-flood	2015_4	0	0	0	1	1	1	3	0	0	0
S5	Post-flood	2015_5	0	1	0	0	7	0	4	0	0	4
S5	Post-flood	2016	0	0	0	0	32	13	13	0	0	0

Table C1. Raw relative abundance of invertebrate data collected at five sites from three streams in Wellington, New Zealand (Chapter 5) between 2004 and 2016. Values are sum number of individuals collected at each site (continued).

Site	Year	*Beraeoptera*	*Chironominae*	*Coloburiscus*	*Costachorema*	*Deleatidium*	*Diamesinae*	Elmidae	Empididae	Ephydridae	*Eriopterini*	*Ferrissia*	*Helicopsyche*
S1	2004	4	0	64	0	249	0	137	0	0	0	0	48
S1	2005	0	0	1033	10	2303	0	468	0	0	5	0	0
S1	2006	1060	0	2607	0	3660	0	1127	0	0	47	0	80
S1	2007	37	11	800	21	2261	0	283	0	0	0	0	53
S1	2008	53	0	555	0	2693	11	491	0	0	16	0	5
S1	2009	35	0	1168	0	1696	0	917	0	0	0	0	123
S1	2010	16	0	160	0	1184	0	144	0	0	0	0	0
S1	2011	96	32	1984	0	192	0	1312	0	0	448	0	32
S1	2012	213	0	11	0	768	0	320	0	0	0	0	11
S1	2013	8	0	116	0	484	0	116	0	0	0	0	36
S1	2014	0	0	640	0	1296	0	432	0	0	0	0	0
S1	2015	176	0	128	0	1488	0	288	0	0	0	0	64
S1	2015_2	0	0	81	0	83	0	25	0	0	0	0	0
S1	2015_3	0	0	21	0	51	0	21	1	0	0	0	0
S1	2015_4	1	0	1	0	15	0	17	0	0	0	0	0
S1	2015_5	2	0	5	0	152	0	43	0	0	0	0	0
S1	2016	32	0	56	0	568	0	80	0	0	0	0	0
S2	2004	0	0	3	0	471	0	306	0	0	5	0	0
S2	2005	8	0	132	0	2495	0	345	0	0	21	0	0
S2	2006	0	0	23	0	406	0	529	0	0	0	0	0
S2	2007	0	96	341	0	2715	496	485	11	0	64	0	0
S2	2008	32	96	448	0	4984	552	2536	0	0	8	0	0
S2	2009	5	27	75	5	1380	0	830	0	0	9	0	0
S2	2010	8	0	80	0	624	0	352	0	0	0	0	0
S2	2011	128	64	16	16	176	0	16	0	0	16	64	112
S2	2012	21	0	21	0	800	0	309	0	0	0	0	0
S2	2013	0	24	32	8	288	0	344	0	0	0	0	0
S2	2014	0	0	21	11	651	0	533	11	0	0	0	0
S2	2015	0	19	0	0	429	0	275	0	0	0	0	0
S2	2015_2	0	0	15	0	313	0	1	0	0	0	0	0
S2	2015_3	2	0	25	0	336	0	48	1	0	0	0	0
S2	2015_4	2	0	47	0	321	0	44	1	0	0	0	0
S2	2015_5	4	0	15	0	716	0	26	0	0	0	0	1

Site	Year	*Beraeoptera*	*Chironominae*	*Coloburiscus*	*Costachorema*	*Deleatidium*	*Diamesinae*	Elmidae	Empididae	Ephydridae	*Eriopterini*	*Ferrissia*	*Helicopsyche*
S2	2016	0	0	16	0	1264	0	112	0	0	8	0	0
S3	2004	0	0	0	3	711	0	28	0	0	0	0	0
S3	2005	0	0	0	0	230	0	566	0	0	0	0	0
S3	2006	0	0	0	0	2020	0	1093	0	0	0	20	0
S3	2007	0	0	27	0	3429	91	1141	0	0	0	0	0
S3	2008	11	0	11	0	3893	11	821	0	0	0	0	0
S3	2009	0	0	8	8	2096	0	616	0	0	0	0	0
S3	2010	0	0	16	16	1280	0	640	0	0	0	0	0
S3	2011	0	0	0	0	16	0	16	0	16	0	0	0
S3	2012	0	0	0	48	672	0	464	0	0	0	0	0
S3	2013	32	0	0	0	1120	0	768	0	0	0	0	0
S3	2014	0	0	0	0	1824	0	768	0	32	0	0	0
S3	2015	0	0	0	0	128	0	32	4	0	0	0	12
S3	2015_2	0	0	1	0	96	0	2	0	0	0	0	0
S3	2015_3	2	1	0	0	283	0	20	0	0	0	0	0
S3	2015_4	2	147	2	0	534	0	12	0	0	0	0	0
S3	2015_5	0	0	0	0	256	0	151	0	0	3	0	0
S3	2016	0	0	0	8	248	0	168	16	8	0	0	24
S4	2004	0	0	4	0	65	0	2	0	0	0	0	0
S4	2005	0	0	9	1	1185	0	30	0	0	1	0	3
S4	2006	0	0	0	9	736	0	117	10	0	0	0	0
S4	2007	0	0	0	16	3008	216	272	40	0	0	0	0
S4	2008	0	43	8	0	187	539	453	0	0	0	0	0
S4	2009	0	0	22	13	1027	0	658	32	32	0	0	0
S4	2010	0	0	0	0	267	0	96	0	0	0	0	0
S4	2011	0	0	0	0	5	0	11	0	0	0	0	0
S4	2012	0	0	0	11	907	0	245	0	0	0	0	0
S4	2013	0	16	32	0	3952	0	272	0	0	0	0	0
S4	2014	0	0	32	0	2880	0	608	0	0	0	0	0
S4	2015	0	0	0	0	352	0	64	0	16	0	0	0
S4	2015_2	0	0	0	0	61	0	13	0	0	0	0	0
S4	2015_3	0	0	2	0	132	0	41	1	0	0	0	0
S4	2015_4	0	2	2	0	284	0	29	0	0	0	0	0
S4	2015_5	0	0	1	0	328	0	166	0	0	0	0	0
S4	2016	0	0	0	16	1888	0	272	0	0	0	0	32
S5	2004	0	0	1	0	123	0	21	2	0	0	0	0

Site	Year	*Beraeoptera*	*Chironominae*	*Coloburiscus*	*Costachorema*	*Deleatidium*	*Diamesinae*	Elmidae	Empididae	Ephydridae	*Eriopterini*	*Ferrissia*	*Helicopsyche*
S5	2005	0	0	5	3	1584	0	12	2	0	0	0	0
S5	2006	0	0	0	0	287	0	92	10	0	0	0	0
S5	2007	0	16	0	16	144	216	408	8	0	0	0	0
S5	2008	0	0	0	0	23	9	265	0	0	0	11	0
S5	2009	0	0	0	0	256	0	696	0	0	0	8	0
S5	2010	0	0	0	64	48	0	432	0	0	16	16	0
S5	2011	0	0	0	0	6	0	19	0	0	0	755	0
S5	2012	0	0	0	16	232	0	160	0	0	0	0	0
S5	2013	0	16	0	0	912	0	256	0	0	0	0	0
S5	2014	0	0	0	32	1472	0	1920	0	0	0	0	0
S5	2015	0	0	0	32	3232	0	1024	0	0	0	0	0
S5	2015_2	0	0	0	0	38	0	6	0	0	0	0	0
S5	2015_3	0	0	0	0	136	0	54	0	0	0	0	0
S5	2015_4	0	0	0	0	82	0	8	0	0	0	0	0
S5	2015_5	0	0	0	0	36	0	24	0	0	0	0	0
S5	2016	0	0	0	0	390	0	83	6	0	0	6	0

Table C1. Raw relative abundance of invertebrate data collected at five sites from three streams in Wellington, New Zealand (Chapter 5) between 2004 and 2016. Values are sum number of individuals collected at each site (continued).

Site	Year	*Hudsonema*	Hydraenidae	*Hydrobiosella*	*Hydrobiosis*	*Hydrochorema*	*Ichthybotus*	Maoridiamesa	*Megaleptoperla*	*Microvelia*	*Mischoderus*	*Molophilus*	Muscidae
S1	2004	0	16	17	7	0	0	0	0	0	0	0	0
S1	2005	0	337	77	70	0	10	0	0	0	0	0	0
S1	2006	40	653	80	53	0	0	0	20	0	0	0	0
S1	2007	0	0	75	117	0	21	0	0	0	0	0	0
S1	2008	0	251	37	11	0	0	0	0	0	0	0	0
S1	2009	0	317	32	67	8	8	0	0	0	0	0	0
S1	2010	0	80	48	16	0	0	0	0	0	0	0	0
S1	2011	0	32	128	32	320	32	0	0	0	0	0	0
S1	2012	0	21	11	11	0	11	0	0	0	0	0	0
S1	2013	0	40	0	0	0	16	0	0	0	0	0	0
S1	2014	0	48	128	16	0	0	0	0	0	0	0	0
S1	2015	0	208	80	0	16	0	0	0	0	0	0	0
S1	2015_2	0	0	5	0	0	0	0	0	0	0	0	0
S1	2015_3	0	0	0	2	0	1	0	0	0	0	0	0
S1	2015_4	0	2	0	0	0	0	0	0	0	0	0	0
S1	2015_5	0	4	0	1	0	2	0	0	0	0	0	0
S1	2016	0	152	88	8	0	0	0	0	0	0	0	0
S2	2004	0	4	0	4	0	0	0	0	0	0	0	0
S2	2005	0	29	0	64	0	0	4	0	0	0	0	0
S2	2006	0	5	0	20	0	0	91	0	0	0	0	0
S2	2007	0	0	0	53	0	0	91	0	0	0	0	0
S2	2008	0	88	0	376	0	0	0	0	0	0	0	0
S2	2009	0	24	0	60	0	0	0	0	0	0	0	0
S2	2010	0	0	0	8	0	0	8	0	0	0	0	0
S2	2011	0	0	0	32	0	0	0	0	0	16	0	0
S2	2012	32	11	0	43	0	0	11	0	0	0	0	0
S2	2013	0	0	0	8	0	0	24	0	0	0	0	0
S2	2014	0	0	0	21	0	0	0	0	0	0	0	0
S2	2015	0	6	0	6	0	0	0	0	0	0	0	0
S2	2015_2	0	0	0	11	0	0	1	0	0	0	0	0
S2	2015_3	0	0	0	8	0	0	0	0	0	0	0	0

Site	Year	*Hudsonema*	Hydraenidae	*Hydrobiosella*	*Hydrobiosis*	*Hydrochorema*	*Ichthybotus*	Maoridiamesa	*Megaleptoperla*	*Microvelia*	*Mischoderus*	*Molophilus*	Muscidae
S2	2015_4	0	0	0	8	0	0	0	0	0	0	0	0
S2	2015_5	0	0	0	0	0	0	0	1	4	0	0	0
S2	2016	0	8	0	40	0	0	0	0	0	0	0	0
S3	2004	0	0	2	17	0	0	2	0	0	0	0	0
S3	2005	0	0	0	16	0	0	0	0	0	0	0	0
S3	2006	0	0	0	80	0	0	0	0	0	0	0	0
S3	2007	37	0	0	219	0	0	0	0	0	0	0	0
S3	2008	0	0	0	102	0	0	0	0	0	0	0	0
S3	2009	0	0	0	96	0	0	8	0	0	0	0	0
S3	2010	0	0	0	64	0	0	160	0	0	0	0	0
S3	2011	0	0	0	784	0	0	0	0	0	0	0	1008
S3	2012	32	0	0	48	0	0	112	0	0	0	0	0
S3	2013	0	0	0	32	0	0	0	0	0	0	0	0
S3	2014	64	32	0	32	0	0	0	0	0	0	0	0
S3	2015	0	0	0	28	0	0	48	0	0	0	0	0
S3	2015_2	0	0	0	3	0	0	0	0	0	0	0	0
S3	2015_3	0	0	0	1	0	0	0	0	0	0	0	0
S3	2015_4	0	0	0	4	0	0	2	0	0	0	0	0
S3	2015_5	0	0	0	4	0	0	0	0	0	0	1	0
S3	2016	0	0	0	48	0	0	0	0	0	0	0	0
S4	2004	0	0	0	12	0	0	0	0	0	0	1	0
S4	2005	0	0	0	42	0	0	0	0	0	13	0	0
S4	2006	0	0	0	38	0	4	0	0	0	15	4	0
S4	2007	0	0	0	312	0	0	144	0	0	32	0	16
S4	2008	0	0	0	8	0	0	37	0	0	16	0	32
S4	2009	0	0	32	22	0	0	0	0	0	16	0	16
S4	2010	0	0	0	43	0	11	21	0	0	0	0	21
S4	2011	0	0	0	187	0	0	0	0	0	0	0	0
S4	2012	0	0	0	53	0	0	0	0	0	0	0	0
S4	2013	0	0	0	0	0	0	0	0	0	16	0	0
S4	2014	0	0	0	32	0	0	0	0	0	0	0	0
S4	2015	0	0	0	0	0	0	32	0	0	0	0	16
S4	2015_2	0	0	1	1	0	0	0	0	0	0	0	0
S4	2015_3	0	0	0	3	0	0	0	0	0	0	0	0
S4	2015_4	0	0	0	1	0	0	0	0	0	0	0	0
S4	2015_5	0	0	0	3	0	0	1	0	6	0	0	1

Site	Year	*Hudsonema*	Hydraenidae	*Hydrobiosella*	*Hydrobiosis*	*Hydrochorema*	*Ichthybotus*	Maoridiamesa	*Megaleptoperla*	*Microvelia*	*Mischoderus*	*Molophilus*	Muscidae
S4	2016	0	0	0	32	0	0	0	0	0	0	0	0
S5	2004	0	0	0	5	0	0	2	0	0	3	0	0
S5	2005	0	0	0	24	0	0	0	0	0	0	0	0
S5	2006	0	0	0	58	0	0	0	0	0	0	0	0
S5	2007	0	0	0	216	0	0	8	0	0	0	0	0
S5	2008	0	0	0	5	0	0	0	0	0	0	0	0
S5	2009	0	0	0	48	0	0	0	0	0	8	0	8
S5	2010	0	0	0	0	0	0	0	0	0	0	0	0
S5	2011	0	0	0	275	0	0	0	0	0	6	0	0
S5	2012	0	0	0	8	0	0	0	0	0	0	0	0
S5	2013	0	0	0	48	0	0	16	0	0	0	0	0
S5	2014	0	0	0	160	0	0	0	0	0	32	0	0
S5	2015	0	0	0	96	0	0	0	0	0	0	0	0
S5	2015_2	0	0	0	0	0	0	0	0	0	0	0	0
S5	2015_3	0	0	0	0	0	0	1	1	0	0	0	0
S5	2015_4	0	0	0	0	0	0	0	0	0	0	0	0
S5	2015_5	0	1	0	0	0	0	2	0	2	0	0	0
S5	2016	0	0	0	58	0	0	6	0	0	0	6	0

Table C1. Raw relative abundance of invertebrate data collected at five sites from three streams in Wellington, New Zealand (Chapter 5) between 2004 and 2016. Values are sum number of individuals collected at each site (continued).

Site	Year	Nematoda	Nemertea	*Neozephlebia*	*Nesameletus*	*Neurochorema*	Oligochaeta	*Olinga*	Orthocladiinae	*Orthopsyche*	Ostracoda	*Oxyethira*	*Paracalliope*
S1	2004	0	0	0	0	0	0	271	0	0	0	0	0
S1	2005	0	0	0	20	5	0	1078	7	0	0	0	10
S1	2006	0	0	20	13	0	20	2773	33	0	0	0	0
S1	2007	0	0	27	0	0	197	2213	0	0	0	0	21
S1	2008	0	0	37	0	0	21	1093	16	0	0	0	5
S1	2009	0	0	8	0	0	56	1579	11	0	0	0	0
S1	2010	0	0	0	0	0	80	1216	16	0	0	0	0
S1	2011	0	0	352	32	0	32	32	32	0	0	0	0
S1	2012	0	0	0	21	0	11	352	21	0	0	0	0
S1	2013	0	0	24	0	0	4	388	4	0	0	0	0
S1	2014	0	0	0	0	0	16	1344	16	0	0	0	64
S1	2015	0	0	16	0	0	16	1008	32	32	0	0	16
S1	2015_2	0	0	0	0	0	0	58	0	1	0	0	0
S1	2015_3	0	0	0	0	0	0	96	0	0	0	0	0
S1	2015_4	0	0	0	0	0	0	12	2	0	0	0	0
S1	2015_5	0	0	0	0	0	0	47	0	0	0	0	0
S1	2016	0	0	0	8	0	8	456	24	8	0	0	0
S2	2004	0	0	0	1	0	0	2	3	0	0	0	6
S2	2005	0	0	0	0	0	9	25	156	0	0	8	22
S2	2006	0	40	0	0	0	30	42	2145	0	0	170	0
S2	2007	0	0	0	0	0	48	11	2427	0	0	0	48
S2	2008	0	0	0	0	0	64	192	448	0	0	0	0
S2	2009	0	4	0	0	0	5	45	330	0	0	0	5
S2	2010	0	0	0	0	0	64	8	184	0	0	0	8
S2	2011	208	48	0	0	16	112	16	16	0	0	0	256
S2	2012	0	0	0	0	11	32	11	43	0	0	0	0
S2	2013	0	0	0	0	0	512	0	112	0	0	0	0
S2	2014	0	0	0	0	0	149	43	235	0	0	0	0
S2	2015	0	0	0	0	0	320	0	166	0	0	0	0
S2	2015_2	0	0	0	0	0	0	8	7	0	0	0	0
S2	2015_3	0	0	0	0	0	0	16	1	0	0	0	0
S2	2015_4	0	0	0	0	0	1	58	7	0	0	0	0
S2	2015_5	0	0	1	0	0	0	16	2	0	0	0	0

Site	Year	Nematoda	Nemertea	*Neozephlebia*	*Nesameletus*	*Neurochorema*	Oligochaeta	*Olinga*	Orthocladiinae	*Orthopsyche*	Ostracoda	*Oxyethira*	*Paracalliope*
S2	2016	0	0	0	0	0	0	8	48	0	0	0	0
S3	2004	2	2	0	0	2	0	2	33	0	0	7	0
S3	2005	0	0	0	16	0	3	15	0	0	5	5	5
S3	2006	0	0	0	0	40	280	93	33	0	233	473	1860
S3	2007	0	0	0	16	0	27	139	181	0	16	0	64
S3	2008	0	0	0	21	0	30	43	87	0	17	6	151
S3	2009	0	0	0	0	8	16	32	160	0	8	32	8
S3	2010	0	0	0	16	0	16	64	80	0	0	0	0
S3	2011	0	0	0	32	16	16	16	64	0	0	48	16
S3	2012	0	0	0	0	32	80	192	192	0	16	0	0
S3	2013	0	0	0	0	0	160	544	64	0	32	0	0
S3	2014	0	0	0	0	0	32	416	288	0	0	0	128
S3	2015	0	0	0	0	0	4	0	60	0	0	0	0
S3	2015_2	0	0	0	0	0	0	0	0	0	0	0	0
S3	2015_3	0	0	0	0	3	1	0	3	0	0	0	0
S3	2015_4	0	0	0	0	4	0	8	41	0	0	0	0
S3	2015_5	0	0	0	0	1	8	4	1	0	0	0	0
S3	2016	0	16	8	0	0	8	40	32	0	0	0	0
S4	2004	0	0	0	1	0	24	0	329	2	0	0	0
S4	2005	0	3	0	3	0	40	3	26	6	1	0	0
S4	2006	0	8	0	0	0	108	0	493	0	24	405	10
S4	2007	8	0	0	0	0	120	0	936	0	8	1088	0
S4	2008	0	0	0	0	0	267	0	1920	0	8	1352	0
S4	2009	0	0	0	0	0	86	0	1188	0	0	522	0
S4	2010	0	0	0	0	0	0	0	0	491	0	235	0
S4	2011	0	0	0	0	0	11	0	75	0	0	53	0
S4	2012	11	0	0	0	0	75	0	0	0	0	11	0
S4	2013	0	0	0	0	0	0	0	0	0	0	0	0
S4	2014	0	0	0	0	0	128	0	32	0	0	0	0
S4	2015	0	32	0	0	0	416	0	1648	0	0	112	0
S4	2015_2	0	0	0	0	0	2	0	4	6	0	0	0
S4	2015_3	0	0	0	0	0	83	2	7	0	0	0	0
S4	2015_4	0	0	0	0	0	42	0	10	0	0	0	0
S4	2015_5	0	0	0	0	0	69	0	132	0	0	1	0
S4	2016	0	0	0	0	0	0	0	64	0	16	16	0
S5	2004	0	0	0	0	0	88	0	686	2	2	0	7

Site	Year	Nematoda	Nemertea	*Neozephlebia*	*Nesameletus*	*Neurochorema*	Oligochaeta	*Olinga*	Orthocladiinae	*Orthopsyche*	Ostracoda	*Oxyethira*	*Paracalliope*
S5	2005	0	0	0	0	0	46	0	20	0	0	0	83
S5	2006	0	13	0	0	0	278	0	1982	0	545	397	447
S5	2007	0	0	0	0	0	544	16	2256	0	16	64	112
S5	2008	0	0	0	0	0	221	0	2079	0	12	12	6
S5	2009	0	0	0	0	0	104	0	1440	0	8	880	40
S5	2010	0	0	0	0	0	160	0	656	0	0	80	16
S5	2011	0	38	0	0	0	19	0	6	0	0	13	0
S5	2012	0	0	0	0	0	192	0	176	0	0	48	0
S5	2013	0	0	0	0	0	0	0	1616	0	0	80	0
S5	2014	0	0	0	0	0	224	0	704	0	32	96	64
S5	2015	0	32	0	0	0	32	0	96	0	0	0	0
S5	2015_2	0	0	0	0	0	7	0	2	0	0	0	0
S5	2015_3	0	0	0	0	0	8	0	9	0	0	0	0
S5	2015_4	0	0	0	0	0	20	0	9	0	0	0	0
S5	2015_5	0	2	0	0	0	95	0	1014	0	1	15	0
S5	2016	13	6	0	0	0	250	0	218	19	13	51	0

Table C1. Raw relative abundance of invertebrate data collected at five sites from three streams in Wellington, New Zealand (Chapter 5) between 2004 and 2016. Values are sum number of individuals collected at each site (continued).

Site	Year	*Peritheates*	*Physa*	Platyhelminthes	*Plectrocnemia*	Polypedilum	*Polyplectropus*	*Potamopyrgus*	*Psilochorema*	*Psychodidae*	Ptilodactylidae	*Pycnocentria*
S1	2004	0	0	0	0	0	0	39	4	0	2	0
S1	2005	0	0	0	0	0	0	10	37	0	0	0
S1	2006	0	0	0	0	0	20	267	53	0	0	13
S1	2007	21	0	0	0	0	0	400	16	0	0	16
S1	2008	0	0	0	0	11	0	5	32	0	11	5
S1	2009	8	0	0	0	0	0	64	8	0	0	0
S1	2010	0	0	0	0	0	0	16	16	0	0	0
S1	2011	32	0	0	0	0	0	32	96	0	512	0
S1	2012	0	0	0	0	0	0	75	0	0	0	0
S1	2013	0	0	0	0	0	0	36	0	0	0	0
S1	2014	0	0	32	0	0	0	16	16	0	0	0
S1	2015	0	0	0	0	0	0	96	0	0	0	0
S1	2015_2	0	0	0	0	0	0	0	6	0	0	0
S1	2015_3	0	0	0	0	0	0	0	2	0	0	0
S1	2015_4	0	0	0	0	0	0	0	4	0	0	9
S1	2015_5	0	0	0	0	0	0	2	0	0	0	0
S1	2016	0	0	0	0	8	0	328	16	0	0	0
S2	2004	0	0	0	0	0	0	2	3	0	0	0
S2	2005	0	0	0	0	60	0	4	41	0	0	0
S2	2006	0	0	10	0	0	0	241	0	0	0	52
S2	2007	0	0	0	0	0	0	181	21	0	0	11
S2	2008	0	0	0	0	32	0	32	8	0	0	64
S2	2009	0	0	11	0	0	0	30	13	0	0	21
S2	2010	0	0	0	0	0	0	40	24	0	0	0
S2	2011	0	0	0	160	0	0	160	16	0	368	80
S2	2012	0	0	0	0	0	0	139	11	0	0	11
S2	2013	0	0	0	0	0	0	8	0	0	0	0
S2	2014	0	0	21	0	0	0	53	11	0	0	0
S2	2015	0	0	6	0	0	0	13	32	0	0	0
S2	2015_2	0	0	0	0	0	0	0	0	0	0	0
S2	2015_3	0	0	0	0	0	0	0	4	0	0	3

Site	Year	*Peritheates*	*Physa*	Platyhelminthes	*Plectrocnemia*	Polypedilum	*Polyplectropus*	*Potamopyrgus*	*Psilochorema*	*Psychodidae*	Ptilodactylidae	*Pycnocentria*
S2	2015_4	0	0	0	0	0	0	0	7	0	0	7
S2	2015_5	0	0	0	0	0	0	0	5	0	0	2
S2	2016	0	0	0	8	0	0	24	8	0	0	0
S3	2004	0	3	0	0	2	0	160	2	0	0	0
S3	2005	0	5	0	0	0	0	554	10	0	0	10
S3	2006	0	60	0	0	0	0	3000	0	0	0	273
S3	2007	0	0	0	0	0	0	1259	0	0	0	571
S3	2008	0	0	0	0	0	0	134	38	0	0	149
S3	2009	0	0	0	0	0	0	288	0	0	0	24
S3	2010	0	0	0	0	0	0	256	32	0	0	32
S3	2011	0	0	16	0	0	16	784	448	0	0	128
S3	2012	0	0	0	0	0	0	256	16	0	0	320
S3	2013	0	0	0	0	0	0	1632	32	0	0	192
S3	2014	0	0	0	0	0	0	352	32	0	0	512
S3	2015	0	0	0	0	0	0	192	12	0	0	4
S3	2015_2	0	0	0	0	0	0	1	4	0	0	0
S3	2015_3	0	1	0	0	1	0	7	3	0	0	5
S3	2015_4	0	1	0	0	2	0	7	6	0	0	3
S3	2015_5	0	0	0	0	0	0	38	2	0	0	1
S3	2016	0	0	0	0	0	0	120	16	0	0	24
S4	2004	0	0	0	0	2	0	29	0	1	0	0
S4	2005	0	0	0	0	0	3	47	12	0	0	0
S4	2006	0	16	0	0	0	0	174	0	4	0	5
S4	2007	0	16	0	0	0	0	1096	0	0	0	0
S4	2008	0	29	8	0	0	0	176	0	8	0	16
S4	2009	0	6	3	0	0	0	448	0	0	0	0
S4	2010	0	0	0	0	0	0	139	0	11	0	0
S4	2011	0	155	32	0	0	0	37	0	0	0	0
S4	2012	0	0	21	0	0	0	565	0	0	0	0
S4	2013	0	0	0	0	0	0	1984	0	0	0	16
S4	2014	0	0	128	0	0	0	3584	0	0	0	0
S4	2015	0	0	32	0	0	0	800	0	0	0	0
S4	2015_2	0	0	0	0	0	0	3	0	0	0	0
S4	2015_3	0	0	0	0	0	0	0	3	0	0	0
S4	2015_4	0	0	0	0	0	0	2	0	0	0	0
S4	2015_5	0	0	0	0	1	0	15	1	0	0	0

Site	Year	*Peritheates*	*Physa*	Platyhelminthes	*Plectrocnemia*	Polypedilum	*Polyplectropus*	*Potamopyrgus*	*Psilochorema*	*Psychodidae*	Ptilodactylidae	*Pycnocentria*
S4	2016	0	16	16	16	0	16	544	0	16	0	0
S5	2004	0	0	0	0	23	0	238	7	3	0	0
S5	2005	0	0	0	0	0	0	17	0	2	0	3
S5	2006	0	23	0	0	0	10	253	0	0	0	0
S5	2007	0	80	72	0	8	0	5256	0	0	0	0
S5	2008	0	16	9	0	0	0	738	0	0	0	0
S5	2009	0	8	0	0	0	0	600	0	0	0	0
S5	2010	0	0	64	0	0	0	784	0	0	0	0
S5	2011	0	83	653	0	0	0	179	0	0	0	0
S5	2012	0	0	16	0	0	0	608	0	0	0	0
S5	2013	0	0	0	0	0	0	224	0	0	0	16
S5	2014	0	0	32	0	0	0	896	0	0	0	0
S5	2015	0	0	32	0	32	0	1184	0	0	0	0
S5	2015_2	0	0	0	0	0	0	11	0	0	0	0
S5	2015_3	0	0	0	0	0	0	3	0	0	0	0
S5	2015_4	0	0	0	0	0	0	1	0	0	0	0
S5	2015_5	0	0	0	0	0	0	18	0	0	0	0
S5	2016	0	6	32	0	13	0	506	0	0	0	0

Table C1. Raw relative abundance of invertebrate data collected at five sites from three streams in Wellington, New Zealand (Chapter 5) between 2004 and 2016. Values are sum number of individuals collected at each site (continued).

Site	Year	*Pycnocentrodes*	*Rallidens*	*Spaniocerca*	*Stenoperla*	Tanypodinae	Tanytarsini	*Zelandobius*	*Zelandoperla*	*Zephlebia*
S1	2004	4	0	0	21	0	0	10	107	0
S1	2005	0	0	0	55	0	0	50	557	0
S1	2006	100	0	0	73	20	13	0	1653	0
S1	2007	0	0	0	101	0	48	43	1435	21
S1	2008	0	0	0	80	0	11	53	672	5
S1	2009	24	0	0	51	0	35	16	517	0
S1	2010	0	0	0	64	0	0	48	368	0
S1	2011	0	0	0	32	0	0	0	64	96
S1	2012	32	0	0	11	0	11	0	277	0
S1	2013	4	0	0	32	0	0	0	4	0
S1	2014	0	0	0	48	0	0	0	144	16
S1	2015	0	0	0	16	0	16	0	320	0
S1	2015_2	0	0	0	2	0	0	0	2	0
S1	2015_3	4	0	0	5	0	0	0	1	0
S1	2015_4	8	0	0	1	0	0	0	0	0
S1	2015_5	7	1	0	3	0	0	0	0	0
S1	2016	0	0	0	32	0	32	0	184	0
S2	2004	2	0	0	0	0	0	0	6	0
S2	2005	0	0	0	0	4	30	0	0	4
S2	2006	413	0	0	0	0	84	0	0	8
S2	2007	27	0	11	0	0	2603	0	27	0
S2	2008	32	0	0	0	0	3400	0	24	40
S2	2009	51	0	0	5	0	68	5	32	0
S2	2010	0	0	0	0	0	88	0	24	0
S2	2011	32	0	0	0	16	3648	0	16	0
S2	2012	192	0	0	0	0	21	0	0	21
S2	2013	16	0	0	0	0	8	0	56	0
S2	2014	21	0	0	0	0	64	0	11	0
S2	2015	0	0	0	0	0	0	0	6	0
S2	2015_2	3	0	4	0	0	4	3	9	0
S2	2015_3	75	0	0	0	0	0	2	1	0
S2	2015_4	58	0	2	0	0	0	15	0	0

Site	Year	*Pycnocentrodes*	*Rallidens*	*Spaniocerca*	*Stenoperla*	Tanypodinae	Tanytarsini	*Zelandobius*	*Zelandoperla*	*Zephlebia*
S2	2015_5	23	1	0	0	0	0	0	0	1
S2	2016	0	0	0	0	0	8	0	0	8
S3	2004	22	0	0	0	0	0	4	4	5
S3	2005	614	0	0	0	10	0	0	34	0
S3	2006	867	0	0	0	0	53	0	0	0
S3	2007	1157	0	0	0	43	69	0	0	16
S3	2008	288	0	0	0	0	60	0	0	0
S3	2009	64	0	0	0	0	0	0	8	0
S3	2010	64	0	0	0	0	48	0	0	0
S3	2011	16	0	0	0	0	48	0	0	0
S3	2012	96	0	0	0	0	112	0	0	0
S3	2013	288	0	0	0	0	0	0	32	32
S3	2014	480	0	0	0	0	352	0	0	0
S3	2015	36	0	0	0	0	4	0	0	0
S3	2015_2	6	0	1	0	0	0	0	0	0
S3	2015_3	73	1	0	0	0	0	1	0	6
S3	2015_4	97	0	4	0	0	6	4	1	15
S3	2015_5	224	0	0	0	0	3	2	0	0
S3	2016	48	0	0	0	0	120	0	0	0
S4	2004	0	0	1	0	1	1	1	4	9
S4	2005	3	0	0	0	5	0	0	6	3
S4	2006	5	0	0	0	14	1913	0	0	0
S4	2007	48	0	0	0	24	408	0	0	0
S4	2008	8	0	0	0	0	229	11	8	11
S4	2009	0	0	6	0	0	432	0	16	0
S4	2010	0	0	0	0	0	192	0	0	0
S4	2011	91	0	0	0	0	107	0	0	0
S4	2012	0	0	0	0	0	0	0	0	0
S4	2013	80	0	0	0	0	0	0	0	0
S4	2014	800	0	0	0	0	0	0	0	0
S4	2015	0	0	0	0	0	16	0	0	0
S4	2015_2	2	0	1	0	3	0	2	2	0
S4	2015_3	34	0	0	0	1	0	0	0	0
S4	2015_4	40	0	2	0	0	0	0	0	0
S4	2015_5	117	0	0	0	0	25	0	0	0

Site	Year	*Pycnocentrodes*	*Rallidens*	*Spaniocerca*	*Stenoperla*	Tanypodinae	Tanytarsini	*Zelandobius*	*Zelandoperla*	*Zephlebia*
S4	2016	400	0	0	0	48	16	0	0	0
S5	2004	0	0	3	0	0	2	5	0	21
S5	2005	0	0	0	0	2	0	0	0	3
S5	2006	0	0	0	0	12	775	0	0	0
S5	2007	64	0	0	0	0	144	0	16	0
S5	2008	0	0	0	0	3	3	0	0	0
S5	2009	0	0	0	0	0	48	0	0	0
S5	2010	0	0	0	0	0	0	0	0	0
S5	2011	26	0	0	0	0	6	0	0	6
S5	2012	0	0	0	0	0	0	0	0	0
S5	2013	32	0	0	0	0	32	0	0	0
S5	2014	96	0	0	0	0	32	0	0	0
S5	2015	256	0	0	0	96	0	0	0	0
S5	2015_2	2	0	0	0	1	0	0	0	0
S5	2015_3	12	0	0	0	0	0	2	0	0
S5	2015_4	7	0	1	0	0	0	0	0	0
S5	2015_5	0	0	0	0	0	4	0	0	0
S5	2016	0	0	0	0	13	13	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site.

Site	Replicates	*Acentrella lata* Muller & Liebenau, 1985	*Acentrella* sp.	*Acroneuria magnifica* Cao & Bae, 2007	*Aeschonophlebia* sp.	*Afronurus meo* Nguyen & Bae, 2003	*Afronurus mnong* Nguyen & Bae, 2003	*Agriocnemis* sp.	*Amphinemura* sp.	*Amphipsyche* sp.	*Anotogaster* sp.	*Antocha* sp.
S1	S1.1	1	1	0	0	0	3	0	3	0	0	0
S1	S1.2	0	0	2	1	7	0	0	1	0	3	1
S1	S1.3	0	0	0	0	0	6	0	0	0	0	0
S1	S1.4	0	0	0	0	0	15	0	0	0	0	1
S1	S1.5	0	0	0	0	0	6	0	0	0	0	1
S2	S2.1	0	0	0	2	2	1	0	0	0	1	0
S2	S2.2	0	0	0	0	0	10	1	0	0	2	0
S2	S2.3	0	0	0	0	18	8	1	0	0	2	0
S2	S2.4	0	0	0	0	0	1	0	0	0	0	0
S2	S2.5	0	0	0	0	0	2	0	0	0	0	0
S3	S3.1	0	0	0	0	0	0	0	7	0	1	0
S3	S3.2	0	0	0	0	1	0	0	2	0	0	0
S3	S3.3	0	0	0	0	0	0	0	5	0	0	5
S3	S3.4	0	0	0	1	0	0	0	3	0	1	0
S3	S3.5	0	0	0	0	2	0	1	0	0	0	3
S4	S4.1	0	0	0	0	2	0	0	0	0	0	1
S4	S4.2	0	0	0	0	1	0	0	0	0	0	5
S4	S4.3	0	1	0	0	0	1	0	0	0	0	13
S4	S4.4	0	0	0	1	0	0	0	0	0	0	4
S4	S4.5	0	0	0	0	0	0	0	0	5	0	3
S5	S5.1	0	2	0	0	18	9	0	0	0	0	40
S5	S5.2	0	0	0	0	3	5	0	0	10	0	20
S5	S5.3	0	0	0	0	3	9	0	0	0	0	6
S5	S5.4	0	0	0	0	8	0	0	0	0	0	17
S5	S5.5	0	0	0	1	7	15	0	0	0	0	11
S6	S6.1	0	0	0	0	0	3	0	0	0	0	17
S6	S6.2	0	0	0	0	8	5	0	0	0	0	14
S6	S6.3	0	3	0	0	3	2	0	0	0	0	4
S6	S6.4	0	0	0	0	8	0	0	0	0	0	3
S6	S6.5	0	0	0	0	10	11	0	1	0	0	2
S7	S7.1	0	1	0	0	5	0	0	0	0	0	0

Site	Replicates	*Acentrella lata* Muller & Liebenau, 1985	*Acentrella* sp.	*Acroneuria magnifica* Cao & Bae, 2007	*Aeschonophlebia* sp.	*Afronurus meo* Nguyen & Bae, 2003	*Afronurus mnong* Nguyen & Bae, 2003	*Agriocnemis* sp.	*Amphinemura* sp.	*Amphipsyche* sp.	*Anotogaster* sp.	*Antocha* sp.
S7	S7.2	0	0	0	0	13	0	0	0	0	0	0
S7	S7.3	0	0	0	0	4	6	0	1	0	2	0
S7	S7.4	0	0	0	0	9	0	0	0	0	0	1
S7	S7.5	0	1	0	0	17	0	0	0	0	0	1
S8	S8.1	0	0	0	0	3	0	0	0	0	0	1
S8	S8.2	1	3	0	0	5	0	0	0	0	0	6
S8	S8.3	0	1	0	0	23	5	0	0	0	0	3
S8	S8.4	0	0	0	0	6	0	0	0	0	0	1
S8	S8.5	0	1	0	0	3	0	0	0	0	0	1
S9	S9.1	0	0	0	0	4	0	1	2	0	0	0
S9	S9.2	0	0	0	0	0	0	0	1	0	0	0
S9	S9.3	0	0	0	0	3	0	0	0	0	0	0
S9	S9.4	0	0	0	0	5	0	0	0	0	0	0
S9	S9.5	0	0	0	0	0	0	0	0	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site (continued).

Site	Replicates	*Apsilochorema* sp.	*Arctopsyche* sp.	*Asionurus primus* Braasch & Soldán, 1986	*Atherix* sp.	*Atractelmis* sp.	*Baetiella bispinosa* Tong & Dudgeon, 2000	*Baetiella* sp.	*Baetis* sp.1	*Baetis* sp.2	*Baetis* sp.3	*Baetis* sp.4
S1	S1.1	0	0	0	0	0	0	0	0	0	3	0
S1	S1.2	0	0	0	0	0	0	0	0	0	0	0
S1	S1.3	0	0	0	0	0	0	0	0	0	0	0
S1	S1.4	0	0	0	0	0	0	0	0	1	0	0
S1	S1.5	0	0	0	0	0	0	0	0	1	0	0
S2	S2.1	0	0	0	0	0	0	0	0	0	2	0
S2	S2.2	0	0	0	0	0	0	0	0	0	1	0
S2	S2.3	0	0	0	0	0	0	0	0	1	0	0
S2	S2.4	0	0	2	0	4	0	0	0	0	0	0
S2	S2.5	0	0	0	0	0	0	0	0	0	0	0
S3	S3.1	0	0	0	0	0	0	0	0	0	0	0
S3	S3.2	0	0	0	0	0	0	0	0	0	0	0
S3	S3.3	0	0	0	0	0	0	0	0	0	1	0
S3	S3.4	0	1	0	0	0	0	0	0	0	1	0
S3	S3.5	0	0	0	0	0	0	0	0	0	0	1
S4	S4.1	0	0	0	0	0	1	0	0	0	0	5
S4	S4.2	0	0	0	1	0	1	0	11	0	13	13
S4	S4.3	0	0	0	0	0	4	2	0	0	5	13
S4	S4.4	0	0	0	0	0	0	0	0	0	5	3
S4	S4.5	0	0	0	0	0	1	0	0	0	2	0
S5	S5.1	0	0	1	0	0	0	0	0	0	4	2
S5	S5.2	0	0	0	0	0	0	0	0	0	3	4
S5	S5.3	0	0	3	0	0	0	0	0	6	8	0
S5	S5.4	0	9	0	0	0	0	0	0	2	6	0
S5	S5.5	0	7	0	0	0	0	0	0	1	1	0
S6	S6.1	0	7	0	0	0	0	0	0	5	0	3
S6	S6.2	0	0	0	0	0	0	0	0	0	0	0
S6	S6.3	0	0	5	0	0	0	0	0	0	10	0
S6	S6.4	0	0	0	0	0	0	0	0	0	9	0

Site	Replicates	*Apsilochorema* sp.	*Arctopsyche* sp.	*Asionurus primus* Braasch & Soldán, 1986	*Atherix* sp.	*Atractelmis* sp.	*Baetiella bispinosa* Tong & Dudgeon, 2000	*Baetiella* sp.	*Baetis* sp.1	*Baetis* sp.2	*Baetis* sp.3	*Baetis* sp.4
S6	S6.5	0	0	0	0	0	0	0	0	0	20	0
S7	S7.1	0	2	0	0	0	0	0	0	0	4	9
S7	S7.2	0	0	12	0	0	0	0	0	0	2	0
S7	S7.3	4	0	7	0	0	0	0	0	0	13	0
S7	S7.4	5	0	1	0	0	0	0	1	0	20	0
S7	S7.5	6	0	0	0	0	0	0	4	0	44	0
S8	S8.1	5	0	0	0	0	0	0	3	0	53	0
S8	S8.2	1	13	0	0	0	0	0	1	0	23	0
S8	S8.3	0	1	0	0	0	0	0	3	0	30	1
S8	S8.4	0	5	0	0	0	1	0	6	0	36	3
S8	S8.5	3	0	0	0	0	0	0	1	0	30	0
S9	S9.1	1	0	0	0	0	0	0	0	0	1	0
S9	S9.2	0	0	0	0	0	0	0	0	0	0	0
S9	S9.3	0	0	0	0	0	0	0	0	0	9	0
S9	S9.4	0	0	0	0	0	0	0	0	0	3	0
S9	S9.5	2	0	0	0	0	0	0	1	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site (continued).

Site	Replicates	*Baetis* sp.5	*Baetis* sp.6	*Bezzia* sp.	*Blephariceraa* sp.	*Brachythemis* sp.	*Brahmana flavomarginata* Wu, 1962	*Caenis cornigera* Kang & Yang, 1994	*Caenis* sp.	*Ceratopsyche* sp.	*Cerion* sp.	*Cheumatopsyche* sp.	*Chimarra* sp.
S1	S1.1	0	0	0	0	0	0	0	0	0	0	0	0
S1	S1.2	0	2	0	0	0	0	0	0	0	0	0	0
S1	S1.3	0	0	0	0	0	0	0	0	0	0	0	1
S1	S1.4	0	0	0	0	0	0	0	0	0	0	0	0
S1	S1.5	0	0	0	0	0	0	0	0	0	0	0	0
S2	S2.1	0	0	0	0	0	0	0	0	0	0	0	0
S2	S2.2	0	0	0	0	0	0	0	0	0	0	0	0
S2	S2.3	0	0	0	0	0	3	0	0	0	1	0	0
S2	S2.4	0	0	0	0	0	0	0	0	0	0	0	0
S2	S2.5	0	0	0	0	0	0	0	0	0	0	0	0
S3	S3.1	0	0	0	0	0	0	0	0	0	0	0	0
S3	S3.2	0	0	0	0	0	0	0	0	0	0	0	0
S3	S3.3	0	0	0	0	0	0	0	0	0	0	0	0
S3	S3.4	0	1	0	0	0	0	0	0	0	0	0	0
S3	S3.5	0	0	0	0	1	0	0	0	0	0	0	0
S4	S4.1	3	2	0	0	0	0	0	0	0	0	4	0
S4	S4.2	0	12	0	0	0	0	0	0	2	0	0	0
S4	S4.3	0	7	0	0	0	0	0	0	2	0	3	0
S4	S4.4	0	0	0	0	0	0	0	0	0	0	1	0
S4	S4.5	0	0	0	0	0	0	0	0	5	0	4	0
S5	S5.1	0	0	0	0	0	0	0	1	18	0	2	0
S5	S5.2	0	0	0	1	0	0	0	1	34	0	31	0
S5	S5.3	0	0	0	0	0	0	1	2	16	0	17	0
S5	S5.4	0	0	0	0	0	0	0	2	45	0	22	0
S5	S5.5	1	0	0	0	0	0	0	0	14	0	9	0
S6	S6.1	6	9	0	0	0	0	0	0	2	0	6	0
S6	S6.2	2	4	0	0	0	0	0	0	0	0	0	0
S6	S6.3	0	2	1	0	0	0	0	0	0	0	1	0
S6	S6.4	0	1	0	0	0	0	0	1	0	0	0	0
S6	S6.5	2	5	0	0	0	0	0	0	0	0	0	0
S7	S7.1	0	0	0	0	0	0	0	0	0	0	0	0

Site	Replicates	*Baetis* sp.5	*Baetis* sp.6	*Bezzia* sp.	*Blephariceria* sp.	*Brachythemis* sp.	*Brahmana flavomarginata* Wu, 1962	*Caenis cornigera* Kang & Yang, 1994	*Caenis* sp.	*Ceratopsyche* sp.	*Cerion* sp.	*Cheumatopsyche* sp.	*Chimarra* sp.
S7	S7.2	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.3	1	0	0	0	0	0	0	0	0	0	0	0
S7	S7.4	0	0	0	0	0	0	0	0	2	0	0	0
S7	S7.5	0	1	0	0	0	0	0	0	0	0	0	0
S8	S8.1	0	0	0	0	0	0	0	0	0	0	0	0
S8	S8.2	0	1	0	0	0	2	0	0	10	0	6	0
S8	S8.3	0	0	0	0	0	0	0	0	0	0	0	0
S8	S8.4	0	0	0	0	0	0	0	0	0	0	4	0
S8	S8.5	0	0	0	0	0	0	0	0	0	0	0	0
S9	S9.1	0	0	0	0	0	0	0	1	1	0	0	0
S9	S9.2	0	0	0	0	0	2	0	0	0	0	0	0
S9	S9.3	0	0	0	0	0	0	0	0	0	0	1	0
S9	S9.4	0	0	0	0	0	0	0	0	1	0	2	0
S9	S9.5	0	0	0	0	0	0	0	1	0	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site (continued).

Site	Replicates	*Chironumus* sp.	*Choroterpes trifurcata* Ulmer, 1939	*Choroterpes vittata* Nguyen & Bae, 2003	*Cincicostella boja* Allen, 1975	*Cincicostella fermorata* (Tshernova, 1972)	*Cincicostella gosei* (Allen, 1975)	*Cincicostella magnusa* Nguyen & Bae, 2013	*Cincicostella notata* Nguyen & Bae, 2013	*Cleptenmis* sp.	*Cyphon* sp.	*Diplonychus* sp.	*Dolophilodes* sp.
S1	S1.1	3	0	0	1	0	0	0	0	0	0	0	0
S1	S1.2	0	0	0	0	0	0	0	0	0	0	0	0
S1	S1.3	1	5	0	0	0	0	0	0	0	1	0	0
S1	S1.4	1	1	0	0	0	0	0	0	0	0	0	0
S1	S1.5	3	7	0	0	0	0	0	0	0	0	0	0
S2	S2.1	3	2	0	0	0	0	0	0	0	0	0	0
S2	S2.2	3	35	0	0	0	0	0	0	0	0	0	0
S2	S2.3	4	42	0	0	0	0	0	0	0	0	0	0
S2	S2.4	4	34	0	0	0	0	0	0	9	0	0	0
S2	S2.5	3	27	0	0	0	0	0	0	9	0	0	0
S3	S3.1	6	3	0	0	0	0	0	0	0	0	0	0
S3	S3.2	18	13	2	0	0	0	0	0	1	0	0	0
S3	S3.3	8	1	2	0	0	0	0	0	0	0	1	0
S3	S3.4	7	1	0	0	0	0	0	0	1	0	0	0
S3	S3.5	17	13	4	0	0	0	0	0	0	0	0	1
S4	S4.1	2	0	0	0	0	0	0	0	1	0	2	0
S4	S4.2	0	1	0	0	0	0	1	6	0	0	0	0
S4	S4.3	1	2	0	2	1	0	0	4	0	0	0	0
S4	S4.4	43	1	0	3	0	0	0	2	0	0	0	0
S4	S4.5	0	0	0	0	0	0	0	2	0	0	0	0
S5	S5.1	2	0	0	0	0	0	0	0	0	0	0	0
S5	S5.2	3	0	0	0	0	0	0	0	2	0	0	0
S5	S5.3	0	0	0	0	0	0	0	1	3	0	0	0
S5	S5.4	4	0	0	0	0	0	0	0	0	0	0	0
S5	S5.5	5	0	0	0	0	1	0	0	6	0	1	0
S6	S6.1	24	0	0	0	0	0	0	3	0	1	0	0
S6	S6.2	7	10	0	0	0	0	0	5	0	0	0	0
S6	S6.3	0	0	0	0	0	0	0	4	0	0	0	0
S6	S6.4	2	1	0	0	0	0	0	1	0	0	0	0
S6	S6.5	2	6	0	0	0	0	0	0	0	0	0	0

Site	Replicates	*Chironumus* sp.	*Choroterpes trifurcata* Ulmer, 1939	*Choroterpes vittata* Nguyen & Bae, 2003	*Cincicostella boja* Allen, 1975	*Cincicostella fermorata* (Tshernova, 1972)	*Cincicostella gosei* (Allen, 1975)	*Cincicostella magnusa* Nguyen & Bae, 2013	*Cincicostella notata* Nguyen & Bae, 2013	*Cleptenmis* sp.	*Cyphon* sp.	*Diplonychus* sp.	*Dolophilodes* sp.
S7	S7.1	0	0	0	0	0	0	0	2	0	0	0	0
S7	S7.2	5	0	0	0	0	0	0	0	0	0	0	0
S7	S7.3	3	0	0	0	0	0	0	0	0	0	0	0
S7	S7.4	3	0	0	0	0	0	0	1	2	0	0	0
S7	S7.5	25	0	0	0	0	0	0	0	12	0	0	0
S8	S8.1	5	0	0	0	0	0	1	0	4	0	0	0
S8	S8.2	1	0	0	0	0	0	0	0	7	0	0	0
S8	S8.3	5	0	0	0	0	0	1	0	0	0	0	0
S8	S8.4	5	0	0	0	0	0	2	0	0	0	0	0
S8	S8.5	3	0	0	0	0	0	0	0	0	0	0	0
S9	S9.1	1	2	0	0	0	0	0	0	0	0	0	0
S9	S9.2	0	2	0	0	0	0	0	0	0	0	0	0
S9	S9.3	0	1	0	0	0	0	0	0	0	0	0	0
S9	S9.4	3	0	0	0	0	0	0	0	3	0	0	0
S9	S9.5	0	0	0	0	0	0	0	0	0	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site (continued).

Site	Replicates	*Drunella ishiyamana* Matsumura, 1931	*Ecdyonurus cervina* Braasch & Soldán, 1984	*Ecdyonurus landai* Braasch & Soldán, 1984	*Ecnomus* sp.	*Entrocorema nigrogeniculatum* (Enderlein, 1909)	*Epeorus aculaetus* Braasch & Soldán, 1990	*Epeorus bifurcatus* Braasch & Soldán, 1979	*Epeorus hieroglyphicus* Braasch & Soldán, 1984	*Epeorus soldani* Braasch & Soldán, 1984	*Epeorus tiberius* Braasch & Soldán, 1984
S1	S1.1	1	0	0	0	2	0	0	5	0	0
S1	S1.2	0	0	0	0	0	0	1	2	0	0
S1	S1.3	0	0	0	0	0	0	0	0	0	0
S1	S1.4	0	0	0	0	0	0	0	1	0	0
S1	S1.5	0	0	0	0	0	0	0	0	0	0
S2	S2.1	0	0	0	0	0	0	1	0	0	0
S2	S2.2	0	0	0	0	3	0	0	0	0	0
S2	S2.3	0	0	0	0	0	0	0	0	0	0
S2	S2.4	0	0	0	0	0	0	0	0	0	0
S2	S2.5	0	0	0	0	2	0	0	0	0	0
S3	S3.1	0	0	0	0	0	0	0	0	0	0
S3	S3.2	0	0	0	0	0	0	0	0	0	0
S3	S3.3	0	0	0	0	0	0	0	0	0	0
S3	S3.4	0	0	0	0	0	0	1	0	0	0
S3	S3.5	0	0	0	0	0	0	1	0	0	0
S4	S4.1	0	0	0	0	2	0	0	0	0	0
S4	S4.2	0	0	0	0	4	0	2	4	0	0
S4	S4.3	0	0	0	0	0	0	0	1	1	1
S4	S4.4	0	0	0	0	2	0	0	0	0	0
S4	S4.5	0	0	0	0	7	0	2	0	0	0
S5	S5.1	0	0	0	0	0	0	1	0	1	5
S5	S5.2	0	0	0	0	0	0	0	1	0	0
S5	S5.3	0	0	3	0	0	0	1	0	0	0
S5	S5.4	0	0	0	0	0	0	5	4	0	5
S5	S5.5	0	7	0	0	0	0	13	12	0	5
S6	S6.1	0	0	0	0	0	0	0	2	0	0
S6	S6.2	0	0	0	11	2	0	0	1	0	0
S6	S6.3	0	0	0	5	0	0	0	3	0	0
S6	S6.4	0	0	0	4	0	0	0	5	0	0

Site	Replicates	*Drunella ishiyamana* Matsumura, 1931	*Ecdyonurus cervina* Braasch & Soldán, 1984	*Ecdyonurus landai* Braasch & Soldán, 1984	*Ecnomus* sp.	*Entrocorema nigrogeniculatum* (Enderlein, 1909)	*Epeorus aculaetus* Braasch & Soldán, 1990	*Epeorus bifurcatus* Braasch & Soldán, 1979	*Epeorus hieroglyphicus* Braasch & Soldán, 1984	*Epeorus soldani* Braasch & Soldán, 1984	*Epeorus tiberius* Braasch & Soldán, 1984
S6	S6.5	0	6	5	1	3	0	0	3	0	0
S7	S7.1	0	0	0	0	0	1	18	6	0	0
S7	S7.2	0	0	0	0	0	0	0	0	0	0
S7	S7.3	0	0	0	0	0	0	1	0	0	1
S7	S7.4	0	0	0	0	0	0	5	1	0	3
S7	S7.5	0	0	0	0	0	1	0	0	0	0
S8	S8.1	0	0	0	0	0	7	34	0	0	0
S8	S8.2	0	0	0	0	0	4	8	42	0	0
S8	S8.3	0	0	0	0	0	1	5	0	0	0
S8	S8.4	0	0	0	0	1	6	35	0	0	1
S8	S8.5	0	0	0	0	0	0	2	1	0	0
S9	S9.1	0	0	2	0	3	0	0	0	0	0
S9	S9.2	0	0	0	0	0	0	0	0	0	0
S9	S9.3	0	0	0	0	2	0	0	0	0	0
S9	S9.4	0	0	0	0	0	1	0	0	0	0
S9	S9.5	0	0	0	0	0	0	0	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site (continued).

Site	Replicates	*Ephemera longiventris* Navás, 1922	*Ephemera* sp.	*Eubrianax* sp.	*Euphaea* sp.	*Glossosoma* sp.	*Goera* sp.	*Gyrinus* sp.	*Habrophlebiodes prominens* Ulmer, 1939	*Heleocoris* sp.	*Helichus* sp.	*Hexatoma* sp.	*Himalopsyche* sp.
S1	S1.1	0	0	2	0	0	0	0	0	2	0	0	1
S1	S1.2	0	0	0	0	0	0	4	0	4	0	0	0
S1	S1.3	0	0	6	0	0	0	0	0	0	0	0	0
S1	S1.4	0	0	5	0	0	0	0	0	0	1	0	0
S1	S1.5	0	0	8	0	0	0	0	1	0	0	0	0
S2	S2.1	0	0	8	0	0	0	0	0	0	0	3	0
S2	S2.2	0	0	19	0	0	0	0	0	1	0	12	0
S2	S2.3	0	0	41	2	0	0	0	3	0	0	5	0
S2	S2.4	0	0	4	3	0	0	0	0	0	0	1	0
S2	S2.5	0	0	10	1	0	0	0	0	0	0	6	0
S3	S3.1	0	0	1	0	0	0	0	1	0	0	1	0
S3	S3.2	0	0	0	0	0	0	0	0	0	0	0	0
S3	S3.3	1	1	0	0	0	0	0	0	3	0	4	0
S3	S3.4	0	0	2	0	0	0	0	0	1	0	0	0
S3	S3.5	0	0	0	0	0	0	0	0	4	0	1	0
S4	S4.1	0	0	1	0	0	1	0	0	0	0	0	0
S4	S4.2	0	3	0	0	0	3	0	0	3	0	1	0
S4	S4.3	0	0	1	0	0	1	3	0	2	0	1	0
S4	S4.4	0	0	5	0	0	1	0	0	1	0	0	0
S4	S4.5	0	2	0	0	1	0	1	0	0	0	3	0
S5	S5.1	0	0	0	0	3	0	0	0	0	0	1	0
S5	S5.2	0	0	0	0	3	0	0	0	1	0	0	0
S5	S5.3	0	0	0	0	0	0	0	0	0	0	0	0
S5	S5.4	0	0	0	1	21	0	0	0	0	0	2	1
S5	S5.5	0	0	0	0	13	4	0	0	0	0	0	0
S6	S6.1	0	0	1	0	1	1	0	0	0	0	4	0
S6	S6.2	0	0	0	0	0	0	1	0	0	0	2	0
S6	S6.3	0	0	1	0	0	0	0	0	0	0	3	0
S6	S6.4	0	0	0	0	16	0	0	0	0	0	1	0
S6	S6.5	0	0	0	0	7	0	0	0	2	0	2	0
S7	S7.1	0	0	0	0	0	0	0	0	0	0	0	0

Site	Replicates	*Ephemera longiventris* Navás, 1922	*Ephemera* sp.	*Eubrianax* sp.	*Euphaea* sp.	*Glossosoma* sp.	*Goera* sp.	*Gyrinus* sp.	*Habrophlebiodes prominens* Ulmer, 1939	*Heleocoris* sp.	*Helichus* sp.	*Hexatoma* sp.	*Himalopsyche* sp.
S7	S7.2	0	0	0	0	0	0	0	0	1	0	0	0
S7	S7.3	0	0	0	0	0	0	0	0	5	0	0	0
S7	S7.4	0	0	0	0	0	0	0	0	5	0	0	0
S7	S7.5	0	0	0	0	0	0	0	0	0	0	1	0
S8	S8.1	0	0	0	0	0	0	0	0	3	0	0	0
S8	S8.2	0	0	0	0	0	0	0	0	0	0	0	0
S8	S8.3	0	0	0	0	0	0	0	1	1	0	0	0
S8	S8.4	0	1	0	0	0	0	0	0	0	0	0	0
S8	S8.5	0	0	0	0	0	0	0	0	14	0	0	0
S9	S9.1	0	0	0	0	5	0	0	0	0	0	0	0
S9	S9.2	0	0	0	0	0	0	0	0	0	0	0	0
S9	S9.3	0	0	0	0	0	0	0	0	0	0	0	0
S9	S9.4	0	0	0	0	0	0	0	0	0	0	0	0
S9	S9.5	0	0	0	0	2	0	0	0	0	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site (continued).

Site	Replicates	*Hydatomanicus* sp.	*Hydropsyche* sp.	*Hydroptila* sp.	*Iron longitibius* Nguyen & Bae, 2004	*Iron martinus* Braasch & Soldán, 1984	*Isca fascia* Nguyen & Bae, 2003	*Isonychia formosana* Ulmer, 1912	*Labiobaetis* sp.1	*Lepidostoma* sp.	*Lype* sp.	*Macrostemum* sp.	*Melanotrichia* sp.
S1	S1.1	1	0	0	3	0	0	0	0	0	0	0	0
S1	S1.2	0	0	0	0	0	0	0	0	0	0	0	0
S1	S1.3	0	0	0	0	0	0	0	0	0	0	0	0
S1	S1.4	0	0	0	0	0	0	0	0	0	0	0	0
S1	S1.5	0	0	0	0	0	0	0	1	0	0	0	0
S2	S2.1	0	0	0	0	0	0	0	0	0	0	0	0
S2	S2.2	0	0	0	0	0	0	0	0	0	0	0	0
S2	S2.3	0	0	0	0	0	0	0	0	0	0	0	1
S2	S2.4	0	0	0	0	0	0	0	0	0	0	0	0
S2	S2.5	0	0	0	0	0	0	0	0	1	0	0	0
S3	S3.1	0	0	0	0	0	0	0	0	3	0	0	0
S3	S3.2	0	0	2	0	0	0	0	0	1	0	0	0
S3	S3.3	0	0	2	0	0	0	0	0	0	1	0	0
S3	S3.4	0	0	0	0	0	0	0	0	0	0	0	0
S3	S3.5	0	0	2	0	0	0	0	0	0	0	0	0
S4	S4.1	0	0	0	0	0	0	2	0	0	0	0	0
S4	S4.2	0	0	0	0	0	0	0	0	0	0	0	0
S4	S4.3	0	3	0	1	2	0	0	1	0	0	0	0
S4	S4.4	0	0	0	0	0	0	0	0	0	0	0	0
S4	S4.5	0	0	0	0	0	0	1	0	0	0	0	0
S5	S5.1	0	0	0	0	0	0	0	0	0	0	0	0
S5	S5.2	0	15	0	0	0	0	1	0	0	0	0	0
S5	S5.3	5	0	0	0	0	0	0	0	0	0	7	0
S5	S5.4	0	11	0	0	0	0	0	0	0	0	0	0
S5	S5.5	0	4	0	0	1	0	0	0	0	0	0	0
S6	S6.1	0	0	0	0	0	1	0	0	0	1	0	0
S6	S6.2	0	0	0	0	0	0	0	0	0	0	0	0
S6	S6.3	0	0	0	0	0	0	0	0	0	0	0	0

Site	Replicates	*Hydatomanicus* sp.	*Hydropsyche* sp.	*Hydroptila* sp.	*Iron longitibius* Nguyen & Bae, 2004	*Iron martinus* Braasch & Soldán, 1984	*Isca fascia* Nguyen & Bae, 2003	*Isonychia formosana* Ulmer, 1912	*Labiobaetis* sp.1	*Lepidostoma* sp.	*Lype* sp.	*Macrostemum* sp.	*Melanotrichia* sp.
S6	S6.4	0	0	0	0	0	0	0	0	0	0	0	0
S6	S6.5	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.1	0	0	0	0	3	0	0	0	0	0	0	0
S7	S7.2	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.3	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.4	0	0	0	0	1	0	0	0	0	0	0	0
S7	S7.5	0	1	0	0	0	0	0	0	0	0	0	0
S8	S8.1	0	0	0	0	0	0	0	0	0	0	0	0
S8	S8.2	0	7	0	4	17	0	0	0	0	0	0	0
S8	S8.3	0	0	0	0	0	0	0	0	0	0	0	0
S8	S8.4	0	1	0	0	0	0	0	0	0	0	0	0
S8	S8.5	0	0	0	0	0	0	0	0	0	0	0	0
S9	S9.1	0	1	0	0	0	0	0	0	0	0	0	0
S9	S9.2	0	2	0	0	0	0	0	0	0	0	0	0
S9	S9.3	0	3	0	0	0	0	0	0	0	0	0	0
S9	S9.4	0	3	0	0	0	0	0	0	0	0	0	0
S9	S9.5	0	1	0	0	0	0	0	0	0	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site (continued).

Site	Replicates	*Micracema* sp.	*Neoperla* sp.	*Neoperlops vietnamellus* Cao & Bae, 2008	*Neumoura* sp.	*Neureclipsis* sp.	*Nigrobaetis* sp.2	*Nigrobaetis* sp.1	*Notacanthella commodema* (Allen, 1971)	*Notacanthella perculta* (Allen, 1971)	*Nyctiophylax* sp.	*Ocetis* sp.
S1	S1.1	0	0	0	1	0	0	0	0	0	0	0
S1	S1.2	0	0	0	0	0	0	0	0	0	0	0
S1	S1.3	0	0	0	0	0	0	0	0	0	0	0
S1	S1.4	0	0	1	0	0	0	0	0	0	1	0
S1	S1.5	0	0	0	0	0	0	0	0	0	0	0
S2	S2.1	0	0	0	0	0	0	0	0	0	0	0
S2	S2.2	0	0	0	0	4	0	1	0	0	0	0
S2	S2.3	1	0	0	1	2	0	0	0	0	0	0
S2	S2.4	0	0	0	3	0	0	0	0	0	0	0
S2	S2.5	1	1	0	0	0	0	0	0	0	0	0
S3	S3.1	1	0	0	0	0	0	1	0	0	0	0
S3	S3.2	0	0	0	0	0	0	0	0	0	0	0
S3	S3.3	0	0	0	0	0	0	0	0	0	0	1
S3	S3.4	0	0	0	0	0	0	0	0	0	0	0
S3	S3.5	0	0	0	0	0	0	0	0	0	0	0
S4	S4.1	0	0	1	1	1	1	0	1	1	0	0
S4	S4.2	0	0	0	2	0	0	0	1	0	0	0
S4	S4.3	0	0	5	1	0	0	1	0	0	0	0
S4	S4.4	0	0	2	0	0	0	0	0	0	0	0
S4	S4.5	0	0	0	0	0	0	0	0	0	0	0
S5	S5.1	0	0	0	0	0	0	0	0	0	0	0
S5	S5.2	0	1	0	0	0	0	0	0	0	0	0
S5	S5.3	0	0	0	1	0	0	0	0	0	0	0
S5	S5.4	0	0	1	0	1	0	0	0	0	0	0
S5	S5.5	0	0	0	0	0	0	0	0	0	0	0
S6	S6.1	0	0	0	0	0	0	1	0	0	0	0
S6	S6.2	0	0	0	0	0	0	2	0	0	0	0
S6	S6.3	0	1	1	0	0	0	1	0	0	0	0
S6	S6.4	0	0	0	0	0	0	0	0	0	0	0
S6	S6.5	0	0	1	0	0	0	0	0	0	0	0

Site	Replicates	*Micracema* sp.	*Neoperla* sp.	*Neoperlops vietnamellus* Cao & Bae, 2008	*Neumoura* sp.	*Neureclipsis* sp.	*Nigrobaetis* sp.2	*Nigrobaetis* sp.1	*Notacanthella commodema* (Allen, 1971)	*Notacanthella perculta* (Allen, 1971)	*Nyctiophylax* sp.	*Ocetis* sp.
S7	S7.1	0	0	0	0	0	0	0	0	0	0	0
S7	S7.2	0	0	0	0	0	0	0	0	0	0	0
S7	S7.3	0	0	0	0	0	0	1	0	0	0	0
S7	S7.4	0	0	0	0	0	0	0	0	0	0	0
S7	S7.5	0	0	0	0	0	0	0	0	0	0	0
S8	S8.1	0	0	0	0	0	0	0	0	0	0	0
S8	S8.2	0	0	0	2	0	0	0	0	1	0	0
S8	S8.3	0	0	0	1	0	0	0	0	0	0	0
S8	S8.4	0	0	0	0	0	0	0	0	0	0	0
S8	S8.5	0	0	0	0	0	0	0	0	0	0	0
S9	S9.1	0	0	0	3	0	0	0	0	0	0	0
S9	S9.2	1	0	0	0	0	0	0	0	0	0	0
S9	S9.3	0	0	0	0	0	0	0	0	0	0	0
S9	S9.4	0	0	0	0	0	0	0	0	0	0	0
S9	S9.5	0	0	0	0	0	0	0	0	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site (continued).

Site	Replicates	*Ophiogomphus* sp.	*Ordobrevia* sp.	*Orectochilus* sp.	*Orthotrichia* sp.	*Oulimnius* sp.	*Paracymoriza* sp.	*Parapoynx* sp.	*Parapyche* sp.	*Pedicia* sp.	*Pericoma* sp.	*Platybaetis bishopi* Muller & Liebenau, 1980	*Polycentropus* sp.
S1	S1.1	0	0	1	0	0	0	0	0	0	0	0	0
S1	S1.2	0	0	0	0	0	0	0	0	0	0	0	0
S1	S1.3	0	0	0	0	0	0	0	0	0	0	0	1
S1	S1.4	0	0	0	0	0	0	0	0	0	0	0	1
S1	S1.5	0	0	0	0	0	0	0	0	0	0	0	7
S2	S2.1	0	1	0	0	0	0	0	0	0	0	0	4
S2	S2.2	0	2	0	0	0	0	0	0	0	0	0	2
S2	S2.3	1	24	3	0	0	0	0	0	0	0	0	2
S2	S2.4	0	0	0	0	0	0	7	0	0	0	0	2
S2	S2.5	0	0	0	0	0	0	0	0	0	0	0	1
S3	S3.1	0	0	1	2	0	0	0	0	0	0	0	3
S3	S3.2	0	0	0	0	0	0	0	0	2	0	0	2
S3	S3.3	0	0	0	0	0	0	0	0	0	0	0	4
S3	S3.4	0	0	0	0	1	0	0	0	0	1	0	12
S3	S3.5	0	0	2	0	0	0	0	0	0	0	0	4
S4	S4.1	2	0	1	0	0	0	0	0	0	0	0	0
S4	S4.2	19	0	1	0	0	0	0	0	0	0	0	5
S4	S4.3	3	0	4	0	0	0	0	0	0	0	0	0
S4	S4.4	7	0	1	0	0	0	0	0	0	0	0	2
S4	S4.5	1	0	2	0	0	0	0	0	0	0	0	3
S5	S5.1	2	0	0	0	0	1	0	0	0	0	0	0
S5	S5.2	1	0	0	0	0	0	0	0	0	0	0	1
S5	S5.3	0	0	0	0	0	0	0	0	0	0	0	1
S5	S5.4	0	0	0	0	0	0	0	0	0	0	0	0
S5	S5.5	0	0	0	0	0	0	0	2	0	0	0	2
S6	S6.1	9	0	3	0	0	0	0	0	0	0	0	0
S6	S6.2	6	0	4	0	0	0	0	0	0	0	0	0
S6	S6.3	3	0	0	0	0	0	0	0	0	0	0	1
S6	S6.4	4	0	0	0	0	0	0	0	0	0	0	0

Site	Replicates	*Ophiogomphus* sp.	*Ordobrevia* sp.	*Orectochilus* sp.	*Orthotrichia* sp.	*Oulimnius* sp.	*Paracymoriza* sp.	*Parapoynx* sp.	*Parapyche* sp.	*Pedicia* sp.	*Pericoma* sp.	*Platybaetis bishopi* Muller & Liebenau, 1980	*Polycentropus* sp.
S6	S6.5	14	0	0	0	0	0	0	0	0	0	0	1
S7	S7.1	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.2	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.3	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.4	0	0	0	0	0	0	0	0	0	0	0	1
S7	S7.5	0	0	0	0	0	0	0	0	0	0	0	2
S8	S8.1	0	0	0	0	0	0	0	0	0	0	0	1
S8	S8.2	0	0	0	0	0	0	0	0	0	0	0	0
S8	S8.3	0	0	0	0	0	0	0	0	0	0	0	0
S8	S8.4	0	0	1	0	0	0	0	0	0	0	0	1
S8	S8.5	1	0	1	0	0	0	0	0	0	0	2	0
S9	S9.1	0	0	0	0	0	0	0	0	0	0	0	0
S9	S9.2	1	0	0	0	0	0	0	0	0	0	0	0
S9	S9.3	0	0	1	0	0	0	0	0	0	0	0	0
S9	S9.4	0	0	0	0	0	0	0	0	0	0	0	2
S9	S9.5	0	0	0	0	0	0	1	0	0	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site (continued).

Site	Replicates	*Potamyia* sp.	*Procloeon spinosum* , Nguyen & Bae, 2006	*Promoresia* sp.	*Prosimulium* sp.	*Protohermes* sp.	*Protonemura* sp.	*Psephelus* sp.	*Psephenoides* sp.	*Psilotreta* sp.	*Psychomyia* sp.	*Rhithrogena parva* Ulmer, 1912	*Rhopalopsole* sp.
S1	S1.1	0	0	0	0	0	3	0	0	0	0	0	0
S1	S1.2	0	0	0	0	0	0	0	0	0	0	0	0
S1	S1.3	0	0	0	0	1	0	0	0	0	0	0	0
S1	S1.4	0	0	0	0	1	0	0	0	0	0	0	0
S1	S1.5	0	0	0	0	0	0	0	0	0	0	0	0
S2	S2.1	0	0	0	0	0	0	0	0	1	0	0	0
S2	S2.2	0	0	0	0	0	1	0	0	2	0	0	0
S2	S2.3	0	0	0	0	0	1	0	0	2	0	0	1
S2	S2.4	0	0	0	0	0	0	3	0	0	0	0	0
S2	S2.5	0	0	0	0	0	0	8	0	1	0	0	0
S3	S3.1	0	0	0	0	1	0	0	0	0	0	0	1
S3	S3.2	0	0	0	0	0	0	0	0	0	0	0	0
S3	S3.3	0	0	1	0	1	1	0	0	0	0	0	0
S3	S3.4	0	0	0	0	0	0	0	0	0	0	0	0
S3	S3.5	0	0	0	0	0	0	0	0	0	0	0	0
S4	S4.1	0	0	4	0	0	0	1	0	0	1	0	0
S4	S4.2	2	0	9	0	0	0	0	0	0	0	0	0
S4	S4.3	0	0	11	0	2	0	0	3	0	0	0	0
S4	S4.4	0	0	0	0	0	0	0	0	0	0	0	0
S4	S4.5	7	0	3	0	1	0	0	4	0	0	0	0
S5	S5.1	5	0	1	0	0	0	0	4	0	0	0	0
S5	S5.2	0	0	7	0	1	0	0	8	0	0	0	0
S5	S5.3	0	0	2	0	0	0	0	3	0	0	0	0
S5	S5.4	0	0	3	0	0	0	0	7	0	0	0	0
S5	S5.5	0	0	1	0	0	0	0	3	0	0	2	0
S6	S6.1	0	0	0	0	1	0	0	1	0	0	0	0
S6	S6.2	0	2	3	0	0	0	0	0	0	0	0	0
S6	S6.3	0	0	1	0	0	0	0	0	0	0	0	0
S6	S6.4	0	0	1	0	0	0	0	0	0	0	0	0
S6	S6.5	0	0	2	0	1	0	0	0	0	0	0	0

Site	Replicates	*Potamyia* sp.	*Procloeon spinosum* , Nguyen & Bae, 2006	*Promoresia* sp.	*Prosimulium* sp.	*Protohermes* sp.	*Protonemura* sp.	*Psephelus* sp.	*Psephenoides* sp.	*Psilotreta* sp.	*Psychomyia* sp.	*Rhithrogena parva* Ulmer, 1912	*Rhopalopsole* sp.
S7	S7.1	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.2	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.3	0	0	0	0	0	0	0	1	0	0	0	0
S7	S7.4	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.5	0	0	0	0	0	0	0	0	0	0	0	0
S8	S8.1	0	0	1	0	0	0	0	0	0	0	0	0
S8	S8.2	0	0	1	0	0	0	0	0	0	0	0	0
S8	S8.3	0	0	0	0	0	0	0	0	0	0	0	0
S8	S8.4	0	0	0	0	1	0	0	0	0	0	0	0
S8	S8.5	0	0	0	0	0	0	0	0	0	0	0	0
S9	S9.1	0	0	0	0	0	0	0	0	0	0	0	0
S9	S9.2	0	0	0	0	0	0	0	0	0	0	0	0
S9	S9.3	0	0	0	0	0	0	0	0	0	0	0	0
S9	S9.4	0	0	1	1	0	0	0	0	0	0	0	0
S9	S9.5	0	0	0	0	0	0	0	0	0	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site (continued).

Site	Replicates	*Rhyacobates* sp.	*Rhyacophila* sp.	*Simulium* sp.	*Sinopsephenus* sp.	*Sphaeronemoura* sp.	*Stenocolus* sp.	*Stenopsyche angustata* Martynov, 1930	*Stenopsyche ulmeri* Navás,1932	*Suragina* sp.	*Tabanus* sp.	*Teloganopsis jinghongensis* (Xu, You & Hsu, 1984)	*Teloganopsis oriens* Jacobus & McCafferty, 2006
S1	S1.1	0	0	11	0	0	0	0	0	0	0	0	0
S1	S1.2	1	0	0	0	0	0	0	1	0	1	0	0
S1	S1.3	0	0	1	0	0	0	0	0	0	0	0	0
S1	S1.4	0	0	1	0	0	0	0	0	0	0	0	0
S1	S1.5	0	0	1	0	0	0	0	0	0	0	0	0
S2	S2.1	0	0	0	2	0	0	0	0	1	0	0	0
S2	S2.2	0	0	0	0	0	0	0	0	0	0	0	0
S2	S2.3	0	0	0	0	0	0	0	0	0	0	0	0
S2	S2.4	0	0	0	0	0	0	0	0	0	0	0	0
S2	S2.5	0	0	1	0	0	0	0	0	0	0	0	0
S3	S3.1	0	0	0	0	0	0	0	0	0	0	0	0
S3	S3.2	0	0	0	0	0	0	0	0	0	0	0	0
S3	S3.3	0	0	0	0	0	0	0	0	0	0	0	0
S3	S3.4	0	0	7	0	1	0	0	0	0	0	0	0
S3	S3.5	0	0	2	0	0	0	0	0	0	0	0	0
S4	S4.1	0	1	0	0	0	0	3	10	0	0	1	0
S4	S4.2	0	1	2	0	0	0	11	2	0	0	0	0
S4	S4.3	0	0	0	0	0	0	4	0	0	0	0	0
S4	S4.4	0	1	0	0	0	0	0	0	0	0	0	0
S4	S4.5	0	0	15	0	0	1	5	0	0	0	0	0
S5	S5.1	0	0	0	0	0	0	0	0	0	0	0	0
S5	S5.2	0	0	0	0	0	1	0	0	0	0	0	0
S5	S5.3	0	0	1	0	0	1	0	0	0	0	0	0
S5	S5.4	0	0	0	0	0	0	0	0	0	0	1	1
S5	S5.5	0	0	0	0	0	0	0	0	0	0	0	0
S6	S6.1	0	0	0	0	0	0	2	0	0	0	0	0
S6	S6.2	0	0	0	0	0	0	5	2	0	0	0	0
S6	S6.3	0	0	0	0	0	0	5	0	0	0	0	1
S6	S6.4	0	0	0	0	0	0	1	2	0	0	0	0
S6	S6.5	0	1	0	0	0	0	0	0	0	0	0	0

Site	Replicates	*Rhyacobates* sp.	*Rhyacophila* sp.	*Simulium* sp.	*Sinopsephenus* sp.	*Sphaeronemoura* sp.	*Stenocolus* sp.	*Stenopsyche angustata* Martynov, 1930	*Stenopsyche ulmeri* Navás,1932	*Suragina* sp.	*Tabanus* sp.	*Teloganopsis jinghongensis* (Xu, You & Hsu, 1984)	*Teloganopsis oriens* Jacobus & McCafferty, 2006
S7	S7.1	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.2	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.3	0	0	0	0	0	0	0	0	0	0	0	0
S7	S7.4	0	0	0	0	1	0	2	0	0	10	0	0
S7	S7.5	0	0	0	0	1	0	0	0	0	4	0	0
S8	S8.1	0	0	0	0	0	0	3	0	0	4	0	0
S8	S8.2	0	0	5	0	0	0	0	2	0	23	0	0
S8	S8.3	0	0	0	0	0	0	1	0	0	2	1	0
S8	S8.4	0	0	0	0	0	0	10	4	0	0	0	0
S8	S8.5	0	0	0	0	0	0	0	0	0	7	0	0
S9	S9.1	0	17	12	0	0	0	0	0	0	0	0	0
S9	S9.2	0	4	2	0	0	0	0	0	0	1	0	0
S9	S9.3	0	2	5	0	0	0	0	0	0	0	0	0
S9	S9.4	0	11	0	0	0	0	0	0	0	2	0	0
S9	S9.5	0	4	0	0	1	0	0	0	0	0	0	0

Table C2. Raw relative abundance of invertebrate data collected at nine sites from three streams in Sapa Highland, Vietnam (Chapter 6) in 2017. Values are sum number of individuals collected from five Surber samples (area = 0.1 m^2) at each site (continued).

Site	Replicates	*Thalerosphyrus vietnamensis* Dang, 1967	*Thraulus bishopi* Peter & Tsui, 1972	*Tinodes* sp.	*Tipula* sp.	*Togoperla* sp.	*Torleya coheri* (Allen & Edmunds, 1963)	*Torleya nepalica* (Allen & Edmunds, 1963)	*Trichomacronema paniae* Malicky & Chantaramongkol, 1991	*Vietnamella thani* (Tshernova, 1972)	*Wormaldia* sp.	*Zaitzevia* sp.
S1	S1.1	0	0	0	0	0	0	0	0	0	0	1
S1	S1.2	0	0	0	1	2	0	0	0	0	0	0
S1	S1.3	6	5	1	1	0	0	0	0	0	0	3
S1	S1.4	0	0	1	4	1	0	0	0	0	0	6
S1	S1.5	0	0	1	3	0	0	1	0	0	0	1
S2	S2.1	0	0	0	1	0	0	0	0	0	0	1
S2	S2.2	0	0	0	7	0	0	0	0	0	0	10
S2	S2.3	0	0	0	4	0	0	0	0	0	0	22
S2	S2.4	0	0	0	3	0	0	0	0	0	0	0
S2	S2.5	0	0	4	4	0	0	0	0	0	0	1
S3	S3.1	0	1	1	2	0	0	6	0	0	0	0
S3	S3.2	0	0	1	0	0	0	0	0	0	0	0
S3	S3.3	0	0	1	0	0	0	1	0	0	0	1
S3	S3.4	0	0	1	0	0	2	0	0	0	0	0
S3	S3.5	0	0	2	0	0	1	1	0	0	2	1
S4	S4.1	0	0	0	0	0	0	1	0	4	0	0
S4	S4.2	0	0	2	5	0	0	0	0	11	0	7
S4	S4.3	0	0	1	2	5	0	0	0	5	0	3
S4	S4.4	0	0	0	1	0	0	0	0	11	0	9
S4	S4.5	0	0	1	0	0	0	0	12	1	0	1
S5	S5.1	0	0	0	0	0	0	0	7	0	1	1
S5	S5.2	0	0	0	2	0	0	0	16	2	0	9
S5	S5.3	0	0	0	1	0	0	0	11	0	0	8
S5	S5.4	0	0	0	1	0	0	0	9	0	0	1
S5	S5.5	0	0	0	3	0	0	0	4	0	0	4
S6	S6.1	0	0	0	13	1	0	0	3	0	1	3
S6	S6.2	0	0	1	9	0	0	0	4	2	0	3
S6	S6.3	0	0	7	1	0	0	0	3	0	0	3
S6	S6.4	0	0	4	12	0	0	0	0	0	1	0
S6	S6.5	0	0	1	7	0	0	0	1	0	0	4

Site	Replicates	*Thalerosphyrus vietnamensis* Dang, 1967	*Thraulus bishopi* Peter & Tsui, 1972	*Tinodes* sp.	*Tipula* sp.	*Togoperla* sp.	*Torleya coheri* (Allen & Edmunds, 1963)	*Torleya nepalica* (Allen & Edmunds, 1963)	*Trichomacronema paniae* Malicky & Chantaramongkol, 1991	*Vietnamella thani* (Tshernova, 1972)	*Wormaldia* sp.	*Zaitzevia* sp.
S7	S7.1	0	0	0	1	2	0	0	0	0	0	0
S7	S7.2	0	0	2	0	0	1	0	0	0	0	1
S7	S7.3	0	0	0	0	0	0	0	0	0	0	3
S7	S7.4	0	0	0	0	0	0	0	0	0	0	5
S7	S7.5	0	0	0	0	0	0	0	0	0	0	11
S8	S8.1	0	0	0	2	0	0	0	0	0	0	4
S8	S8.2	0	0	0	5	0	0	0	2	0	0	9
S8	S8.3	0	0	0	0	0	0	0	0	0	0	6
S8	S8.4	0	0	0	0	0	0	0	3	0	0	3
S8	S8.5	0	0	0	0	0	0	0	0	0	0	5
S9	S9.1	0	0	0	0	0	0	0	1	0	0	2
S9	S9.2	1	0	0	0	0	0	1	0	0	0	0
S9	S9.3	0	0	0	0	2	0	0	0	0	0	1
S9	S9.4	0	0	0	0	9	0	4	1	0	0	1
S9	S9.5	0	0	0	0	0	0	5	0	0	0	0