Spatial and environmental patterns of rare lotic macroinvertebrate diversity

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To my family, who stood by my side all these years,

and to the memory of my father, who introduced me to the wondrous world of biology.

Abstract

Stream macroinvertebrate communities comprise a few common taxa and many rare ones. Small populations of rare taxa can be more vulnerable to environmental change than those of common taxa. However, they are often discarded from community analyses on the grounds that they complicate data interpretation. The aim of this thesis was to evaluate the effect of rare taxa on assessing ecosystem health and on interpreting biodiversity patterns based on lotic macroinvertebrate communities. I assessed the effect of multiple types of rare taxa exclusion on biomonitoring, using macroinvertebrate data collected for the National River Water Quality Network of Aotearoa New Zealand. I compared the effect of different sampling methods on biodiversity patterns of rare taxa in pristine streams in the Tongariro National Park and determined the local environmental variables most strongly linked with common and rare taxa. Finally, I evaluated the effect dispersal processes and local environment have on structuring the common and rare components of lotic communities, considering the position within the stream network and the dispersal mode of the invertebrates. Exclusion of rare taxa led to significant misclassifications of ecological quality by biomonitoring tools that use presence-absence data, such as the Macroinvertebrate Community Index, and often masked their relationship with nutrient stressors. Different sampling methods collected clearly differentiated rare components of lotic assemblages, depending on the habitat sampled (riffles, non-riffles) and the life-stage of the invertebrates (benthic larvae, flying adults). A comprehensive species inventory can be compiled by combining methods, with benthic samples as the basis. Biodiversity metrics of the common and rare components of macroinvertebrate communities were related to similar environmental variables. While the structure of the two components was related to different variables, in combination they revealed a greater number of relationships with the environment. Rare taxa assemblages were not structured

clearly by either local environment or dispersal processes, however their inclusion was necessary to demonstrate that the complete communities were determined by the local environment. Overall, I did not find any reason to exclude rare taxa from lotic macroinvertebrate studies, but rather found they can facilitate community analyses. Given the increasing threats on lotic macroinvertebrate biodiversity, it is also crucial to include them in such studies, hopefully so we can prevent their complete extinction.

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"As you set out for Ithaka
hope your road is a long one,
full of adventure, full of discovery"
Constantine P. Cavafy

Preface

This PhD thesis comprises four research chapters that have been written as standalone manuscripts and are intended for publication in scientific journals, along with an introductory and a synthesis chapter. Consequently, there is some unavoidable repetition in their content. Numbers of figures and tables indicate the chapter they belong to and their order within it, restarting for each chapter.

All chapters are primarily my own work, with input from my supervisors. I planned the research, carried out field and lab-work, analysed the data and wrote the manuscripts. My chief supervisor, Professor Russell Death, provided guidance on concept and research questions development, methodology, administration, manuscript development and editing in all chapters. As such he is a co-author in all manuscripts. My co-supervisor, Dr. Ian Henderson provided guidance on macroinvertebrate identification, statistical analyses and manuscript development for chapters three and four and thus he is a co-author in these manuscripts. Statements of author contributions are in Appendix E.

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Abbreviations

AcTe	Active Terrestrial dispersers
CCA	Common Caddisfly Assemblage
CI	Confidence Interval
CIA	Common Invertebrate Assemblage
CVM	Central Volcanic Massif
DRP	Dissolved Reactive Phosphorus
EfNSp	Effective Number of Species
HW	Headwaters
MCI	Macroinvertbrate Community Index
MS	Mainstem
NOx	Oxidised Nitrogen
NSp	Number of Species
PaAq	Passive Aquatic dispersers
PaTe	Passive Terrestrial dispersers
PLSR	Partial Least Square Regression
QMCI	Quantitative Macroinvertebrate Community Index
RCA	Rare Caddisfly Assemblage
RCC	River Continuum Concept
REv	Relative Evenness
RIA	Rare Invertebrate Assemblage
SS	Sum of Squares
TCA	Total Caddisfly Assemblage
TIA	Total Invertebrate Assemblage
VIP	Variable Importance in Projection

Chapter 1

Introduction

Rarity is common. Counterintuitive as it may seem, natural communities comprise a few abundant and many rare species (Magurran & Henderson, 2003; Williams, 1944). Even from the time of the voyage of the Beagle, Charles Darwin had noted that rarity was characteristic of most species, in many places and in a variety of taxonomically distinct taxa (Darwin, 1859). Species abundance distributions, almost universally, form a hyperbolic curve, starting with a few, highly abundant, species and continuing with many species of low abundance (McGill et al., 2007; Spitale, 2012). Consequently, a large component of species richness will be from rare species (Cao et al., 1998), and this is also the case for stream macroinvertebrate communities (Lenat & Resh, 2001).

This introduction sets out to list the multiple answers to the question what rarity is, and to explain why this phenomenon is ever present in nature and research datasets. Then, considering the particular characteristics of rare species, it summarises the reasons for focusing on these species, the problems that come with it at different stages of the research process, and the different kinds of responses by researchers in the freshwater ecology field. Finally, it summarises results from studies that attempted to answer whether rare species are useful in freshwater community studies.

1.1 What is rarity?

The concept of rarity has many definitions, describing different natural patterns and will always be set in terms of relative, rather than absolute, differences between species (Preston, 1948; Reveal, 1981). Despite lacking a precise and universal definition, the concept of rarity can be considered accurate by default, only to indulge a need for precision, without accounting for its multifaceted nature (Heywood, 1988). As Gaston (1994) noted in the beginning of his book devoted to rarity, “most species are probably rare according to one definition or another”. Rabinowitz (1981) attempted to

conceptualize rarity as an attribute by evaluating three axes of species distribution, based on different scales of analysis; local density, habitat specificity and geographical range. Her work resulted in "Seven forms of rarity" (Table 1.1).

These three axes are not the only factors that might affect whether a species is considered rare or not though. Different spatial and temporal scales can also affect this distinction (Gaston, 1997). Natural ecosystems are not characterised by absolute uniformity and stability, but rather by patchiness and regular and irregular change. Species that thrive in one space and time, can be considered rare in a different place and/or time (Dee et al., 2019; Magurran & Henderson, 2003). Stochasticity can also play a role. Individuals of a species might drift from their natural habitat to one characterised by non-ideal conditions – vagrant species. Different life-stages of a species might also occupy different niches and affect their rarity status in different habitats (Gaston, 1994).

From a more practical perspective, rarity might be considered a proxy for occurrence probability and/or detectability; rare individuals are by default expected to be difficult to find, because of their low numbers, their uncommon (or inconvenient for the researcher) behaviour, or their clumped distribution, even over large ranges (McDonald, 2013). In all these cases, the precise definition of rarity might be affected by the particular research needs; e.g. policy requires absolute descriptions to apply conservation measures and thus, rarity might be required to be considered as a categorical variable across the whole range of the species, instead of a continuous variable (Violle et al., 2017).

Table 1.1: Seven forms of rarity based on geographical range, habitat specificity and local abundance (Rabinowitz, 1981). The one form of overall commonness (upper left corner) is characterised by widespread, abundant, habitat generalists.

	Geographic range	Large		Small	
	Habitat specificity	Wide	Narrow	Wide	Narrow
Local population size	Large	Locally abundant over a large range in several habitats	Locally abundant over a large range in a specific habitat	Locally abundant in several habitats but restricted geographically	Locally abundant in a specific habitat but restricted geographically
	Small	Constantly sparse over a large range and in several habitats	Constantly sparse in a specific habitat but over a large range	Constantly sparse and geographically restricted in several habitats	Constantly sparse and geographically restricted in a specific habitat

1.1.1 Abundance rarity

As Gaston (1994) pointed out, the lack of a universal definition of rarity, inevitably leads to a lack of a universal methodology to separate common and rare species. However, he suggested the first quartile of the proportionately least abundant species to be considered rare. But such a limit does not take account of any particularities of a certain ecosystem and might conceal the relative differences in the rare component of species richness in different ecosystems (Magurran, 2004). While it does take account of the rare species, it does not acknowledge the presence of many species of low abundance, that will not be considered rare, but may differ from common species. Coddington et al. (2009) in their study on tropical arthropods, sampled assemblages in which rare species extended well into the proposed 75% of the not rare species. The shape of the species abundance distributions might follow some general rules, but it might still vary enough to distinguish different communities on the grounds of their rare species components, be it a product of the spatiotemporal scale of study, sampling methodology or intensity (Magurran & Henderson, 2011).

Even within the abundance criterion, there can be variation in the definition of rarity depending on the research question. It is possible to distinguish between more than two rarity classes, i.e. not just common and rare species (Carney, 1997). Different measures or proxies of abundance (e.g. biomass) can be used, giving different results. Towards the low-abundance end of the cut-off points' spectrum, singletons (species recorded from only one individual) might be the only species considered as rare (Magurran, 2004). However, they might be affected by factors unrelated to the ecology of the said species, such as sampling duration, effort, scale or stochasticity (Magurran & Henderson, 2011).

1.1.2 Relative abundance rarity

There are certain taxonomic groups, whose absolute abundance cannot be measured, and even if it could, they would possibly not qualify for any of the rarity definitions set by absolute abundance limits as they can be very abundant (Cao et al., 1998). In aquatic ecosystems, this is common among small-sized species, such as freshwater macroinvertebrates, zooplankton or phytoplankton. In community studies, rarity of a taxon can be defined in terms of relative abundance, based on the total abundance of the community/ies or the abundance of the most common taxon in a sample or a study, that will itself be only a small part of the habitat it was collected in. The rank-abundance curve can offer another option to distinguish assemblages of common and rare species, which can be comparable between different studies, by using the inflection point (Siqueira et al., 2012). This is located in the region of the rank-abundance curve where the curvature changes. The use of the inflection point will give less zero-inflated matrices in comparison to for example an absolute abundance limit. It can be based either on absolute

or relative abundance and its exact location can be flexible, as moderate shifts in the relative abundance matrices will not affect the general patterns (Magurran, 2004).

1.1.3 Spatial rarity

In cases of studies where independently collected datasets are merged, such as meta-analyses, often working on large scales (regions, countries, continents) and with a multitude of sampling methods, abundances might not be comparable, and thus not useful. In other cases (such as museum datasets), only the presence of a species is available, of interest, or feasible logistically, and thus the data are recorded binary, as presence-absence (even though absence is difficult to confirm, and thus is often interpreted as non-presence). In such cases, rarity will be spatially evaluated and based on the occupancy of a given area by each species. However, the size of the study grid (i.e. the scale) can be a confounding factor. Common and rare species might follow different patterns when scaling up or down, i.e. when the detail in the data is increased or reduced (He & Condit, 2007). But spatial rarity also offers the advantage of comparable studies at different scales in terms of total study area size (Nijboer & Verdonschot, 2004).

As always, whether rarity is defined based on the abundance or distribution of a species depends on the research question and the potential cause(s) of rarity. As (Nijboer & Verdonschot, 2004) noted in their study on aquatic macroinvertebrate rarity, pollution and habitat degradation lead to unfavourable environmental conditions for some species. This makes rarity a local attribute, as those species disappear from degraded sites, instead of persisting at low abundances. Where the environmental conditions are favourable, the abundances of the same species can be high. Thus, an impact study should focus on the rare species' distribution range instead of abundance, to ensure that affected species will be included in the assessment. The inverse of occurrence (i.e. the inverse of the number

of sites where a species is present) can also be used as a proxie for rarity (Mobaied et al., 2015).

1.1.4 Temporal rarity

A species can be rare if it occurs occasionally in an area, irrespective of its abundance (Resh et al., 2005; Robinson et al., 2000). Despite its unquestionable usefulness in evaluating monitoring results and/or developing conservation plans, temporal rarity appears to be rare itself among the definitions used in the literature (Gaston, 1994), a fact that could be attributed to the limited number of long-term studies evaluating this aspect of rarity (Resh et al., 2005). Even though one species that is considered rare at some point in time can become common as a result of a change in environmental conditions (Dee et al., 2019), such species are usually the exception rather than the rule (Magurran & Henderson, 2003; Sgarbi & Melo, 2018). Such a pattern might be more related to the taxonomic group under question, e.g. microbial communities (Debroas et al., 2015).

1.1.5 Functional rarity

Each species performs a function in its environment, and its relevant traits can be either "effect traits", related to its effect on the environment, or "response traits", describing its response to the environment (Violle et al., 2017). Three overarching models have been proposed to describe the relationship between species diversity and ecosystem function (Flather & Hull Sieg, 2007); the complementarity hypothesis suggests that different niches lead to different resource use and thus every species is unique in its contribution to ecosystem function; the redundancy hypothesis suggests that species can replace each other's contribution to ecosystem function; and finally, the facilitative hypothesis

suggests that higher diversity leads to more positive species interactions, consequently increasing ecosystem function.

Functional rarity will be expected to be related to other forms of rarity, such as low abundance and/or limited distribution. Violle et al. (2017) created a typology of functional rarity, equivalent to Rabinowitz's (1981), which assessed species based on abundance, distribution and trait distinctiveness gradients. They distinguished 12 forms of functional rarity, ranging from rare traits, found in a few rare and spatially limited species, to common traits, found in many abundant and widely distributed species. The most common type was evaluated to be the rare species with common traits, while abundant species, dominant in their communities, but with distinct traits were the least frequent. Among freshwater macroinvertebrates, an example of rare functional trait is the absence of fully developed wings in insect species, such as several stonefly species of the family Gripopterygidae in New Zealand, which may have evolved in response to cold conditions and or as a result of isolation (Winterbourn, 1980).

1.1.6 Combinations of rarity types

As has been established by (Rabinowitz, 1981) work, rarity can result from the combination of multiple factors. Distribution and abundance are often positively correlated (Gaston, 1998; Hanski, 1993; Vilmi et al., 2019 but see Gillett et al., 2011), and species with wide distribution and low abundance are rather unusual (Arscott et al., 2006). Hessen & Walseng (2008) found that in general rare lake zooplankton species qualify for more than one rarity criterion. Gillett et al. (2011), in their study on freshwater diatoms, distinguished three kinds of rare taxa based on relative abundance and occurrence; satellite taxa with low abundances and occurrence; rural taxa, widespread with low abundance; and urban, spatially limited, but dominant. Even when changing rarity status, an originally common species can show an (almost) simultaneous decline in

abundance and occupancy (Gaston & Fuller, 2008). Such relationships turn the focus on species with limited distributions and low local abundances, which are potentially in greatest danger of extinction and thus, deserve attention (Neeson et al., 2018). Apart from combined rarity types within species, there can be different species within a community qualifying for different rarity criteria. Longino et al. (2002), for example, found in the same communities of tropical ants, species on the edge of their distribution range, species that were rare as sampling artefacts, and globally rare or even unique species.

1.2 Causes of rarity

After considering what a rare species is, the next important question is why is a species rare? McCreadie & Adler (2008) considered finding a single cause of rarity, a utopia. Gaston (1994) noted that the absence of experimental studies focusing on the phenomenon of rarity has hindered our attempts to understand it. This has led to community studies attempting to describe nature being mostly based on common species, or at least not taking in account the rare species' characteristics. Thus, these studies often fail to describe the role that rare species play in natural communities.

1.2.1 Environmental conditions

Every species has a set of environmental conditions which are ideal for it to live and reproduce and a wider set that allows survival but are not necessarily ideal for its reproduction. Rare species might be limited by several factors, such as physical and chemical environmental conditions. They might also be constrained by being adapted to some specific and rare, or fragmented habitat, or specific biotic interactions (Gaston, 1994; Legalle et al., 2005). Rare species are often found to be specialists, regarding the resources they can most efficiently use (Mobaied et al., 2015; Vermeij & Grosberg, 2018). However, this can also be an artefact related to the availability of the resource (Devictor

et al., 2010). When their preferred resources are rare and the species cannot take advantage of alternative resources, then the species will be rare as well (Spitale, 2012). Vilmi et al. (2019) found that more marginal niches were characteristic of rare freshwater diatom and macroinvertebrate species.

Scale can affect the rarity status of a species. When a study focuses on ecosystems with marginal conditions, such as alpine streams, rarity patterns might differ and be less prevalent than in ecosystems with less extreme conditions (Alther et al., 2019). But in a larger scale study, species that are adapted to such marginal ecosystems where they might be common, might be considered rare. Environmental conditions are also subject to human impact. Land use change, habitat loss and degradation, non-native species' introductions, pollution, human exploitation are all well-known factors that can lead to the decline of biodiversity and consequently render many species rare (Flather & Hull Sieg, 2007).

1.2.2 Species traits and dispersal

The traits that a species has, allow it to survive and reproduce. Common and rare species might differ in traits related to reproductive success, number of offspring per reproductive round, number of reproductive rounds per year, number of reproductively active years, competition, resource usage, trophic levels, body sizes or habitat specialization (Sgarbi & Melo, 2018). Some traits might come with lower abundances by default, such as large predators in comparison to lower trophic levels (Nijboer & Verdonschot, 2004). Rare trait combinations are also possible and can be indicative of rare species, e.g. successful reproduction in rare habitats will lead to rare species as well (Vermeij & Grosberg, 2018).

Several traits (e.g. body size, wing length etc) might be related to the species' dispersal capabilities. Small body size is often related to low active dispersal, limiting species' distribution (Gaston, 1994) and ability to search for new habitats under

environmental change. However, small species might show increased passive dispersal, relying on stochastic factors (e.g. small insects might disperse at long distances, carried by the wind). Rare species are often considered weak dispersers, unable to locate resources beyond their dispersal ability (Spitale, 2012). However, a strongly dispersing species might be able to travel far from its habitat of origin and through mass effects end up in areas with non-ideal environmental conditions. Despite being a strong disperser and possibly common under favourable conditions, being an incidental, transient or vagrant species can render it rare (Gaston, 1994; Spitale, 2012; Vermeij & Grosberg, 2018).

1.2.3 Evolutionary

If rarity is considered a characteristic of a species, i.e. the species does not reach high abundance under any circumstances, then it may be a product of evolution. While it would not be possible for natural selection to act on rarity as an adaptation for survival and reproduction, it can favour traits that take advantage of low abundances or sparse populations in order to counterbalance extinction potential (Rabinowitz, 1981; Vermeij & Grosberg, 2018). For example, tropical forest trees take advantage of being rare by producing seedlings that are such a rare food source, that they have no specialized enemies, such as herbivores or microbes (Bachelot et al., 2016).

1.2.4 Sampling artefact

Rarity might not even be an ecological attribute but an artefact of the sampling protocols. Sampling method may radically affect the rare component of an assemblage (Longino et al., 2002). Bigger samples (in terms of duration, effort or area covered) usually contain more species as predicted by the species-area relationship, and consequently more rare species, some of them might be vagrants (Cao et al., 2001; Heatherly et al., 2007; Magurran & Henderson, 2011). A protocol that targets an assemblage with specific

ecology, e.g. freshwater benthic macroinvertebrates, might collect, and consequently define as rare, species that might be abundant in an adjacent habitat, such as the water column or surface, or species that can evade being sampled, because they are strong swimmers or flyers (Nijboer & Verdonschot, 2004; Sgarbi & Melo, 2018). The scale of the study can also affect the rarity status of a species, if it is defined in terms of relative abundance or distribution (Carmona et al., 2017). The taxonomic level can reveal or mask rare species, and in the case of freshwater macroinvertebrates it may vary a lot among studies (Lenat & Resh, 2001). Rare species identified only to the genus or family level will be masked by their more common congenerics or confamiliars. The taxonomic level may vary even within the same group or study, depending on the researcher's experience or the life-stage of the animals (Resh et al., 2005).

1.3 Importance of rare species for their ecosystems and ecosystem management

Rare species are clearly present in all communities. However, whether they are important components of these communities remains unclear and often sparks passionate debate (Cao et al., 1998, 2001; Cao & Williams, 1999; Marchant, 1999, 2002).

1.3.1 Species richness, monitoring and conservation

It is evident from the species abundance distribution of almost any community, that rare species constitute a substantial component of a community's species richness and consequently affect it more than they do the community's diversity. Despite its limitations in interpretation of natural patterns, species richness is often used in theoretical and applied ecological contexts. In aquatic ecosystems, it has often been shown to reliably follow the ecosystem condition and indicate degradation (Cao et al., 1998). Ecosystem conservation and management might even be facilitated by patterns in assemblages with

data at higher taxonomic levels like genus, family or even order in the most diverse regions (Heino, 2008).

Rare species are, from a biomonitoring perspective, often considered closer to disappearing from an ecosystem or going extinct (Mouillot et al., 2013), even though this varies among species and taxonomic groups (Vermeij & Grosberg, 2018). Rare aquatic macroinvertebrates in a stream sample covering a small area of the streambed might be numerous along a long reach of a river. Rare species are also not always specialists that disappear first after adverse environmental change; in their study on river macroinvertebrates, Arscott et al. (2006) found that anthropogenic impact applied higher stress on, otherwise ubiquitous, sensitive generalist species.

1.3.2 Functional diversity & ecosystem services

While a big component of species richness will be based on rare species, their respective abundances will be much lower. In communities like benthic macroinvertebrates, the same pattern will be seen for their biomass. But biomass is often considered a proxy for a species function in the ecosystem (Violle et al., 2017). Consequently, rare species are often considered by default to contribute less to ecosystem function and services than common species (Alther et al., 2019; Daam et al., 2019; Neeson et al., 2018).

Mouillot et al. (2013) and Violle et al. (2017) focused on functional diversity and suggested that rare functional profiles belonged to the rare species of benthic macroinvertebrates, contributing disproportionately to their communities' functional diversity. Rare functional trait combinations can lead to a release from competition, within and among species, by exploiting different resources (Violle et al., 2017). However, they did not evaluate rare species' contribution to ecosystem function and

services. Rather, they considered rare species as functional back-up against future stressors, which may require different sets of traits.

Focusing on the function that species perform in their ecosystems, Lyons & Schwartz (2001) found rare grass species contributing to ecosystem function against the invasive non-native species by occupying niches that would otherwise be occupied by the invaders. In a study on freshwater protists, Debroas et al. (2015) showed that rare taxa were not just lying dormant, waiting for favorable conditions to reactivate and multiply, as is often thought. Rather, some were always active, contributing to the ecosystem function. Dangles & Malmqvist (2004) found that detrital processing in streams was highest in species rich, but highly uneven, communities, i.e. with many rare species. Dominant species were still responsible for the bulk of the functioning, but the effect on ecosystem function differed for abundant and efficient species. Irrespective of efficiency, a low-abundance or rare species can still contribute several thousand individuals along a stream reach, which will be considered few only relatively to the common species, but can influence their environment.

Dee et al. (2019) reviewed the rare species' effect on ecosystem services and found that they can contribute substantially, directly and indirectly to ecosystem services, also because they tend to have a more unique set of functional traits and roles in the ecosystem than common species. Certain ecosystem services might even be positively affected by the fact that rare species are rare, but they are usually related to human activities, e.g. ornamental species, pets, trophies or luxury products (Dee et al., 2019).

1.4 Reasons to study rare species

1.4.1 Laying the groundwork for studies on rare species

Before attempting to use rare species in applied research, pilot studies need to be conducted to standardise methodology. The definition of rarity can be based on a

somewhat arbitrary cut-off point. To reduce or manage this arbitrariness, reference sites can be used to delineate the natural patterns of abundance or occupancy distributions of rare species, and set the base for future studies (Flather & Hull Sieg, 2007).

1.4.2 Monitoring

According to the taxon cycle (Ricklefs & Cox, 1972), species that remain rare over long timescales (in the order of 10^6 years, Ricklefs & Bermingham, 2002) are generally expected to be heading to extinction (Sgarbi & Melo, 2018). Their populations might remain small and in isolation from each other, exacerbating the effect of inbreeding, while also making the species more vulnerable to disturbance (Gaston & Kunin, 1997). However, not all rare species are threatened (Gaston, 1994). Chronically rare species might be adapted to being rare and thus, common species whose populations are declining (Carmona et al., 2017) might require more urgent conservation measures (Gaston & Fuller, 2008). Cao & Hawkins (2005) in their stress simulation study showed that initially abundant, but sensitive, species were the ones to decline most in the community. Rare species might be resistant to certain types of disturbance and take advantage of the decline of abundant species (Hawkins et al., 2000). Chapman (1999) suggested studies on rare species could shed light on the conditions that allow them to sustain their populations. This knowledge could inform conservation management strategies to mitigate dwindling populations of otherwise common species.

When focusing on short temporal scales, rare species might indeed disappear first. As they will lack the numbers or range to resist novel environmental conditions, any impacts on them will affect their persistence and thus drive biodiversity change (Dee et al., 2019; Resh et al., 2005; Vermeij & Grosberg, 2018). Environmental change can also

lead common species to abruptly become rare and vice versa, further changing the community structure (Magurran & Henderson, 2011).

Biomonitoring is to a large extent a study on whether a species is present in an ecosystem or not. However, the absence of a species is often difficult to confirm (MacKenzie et al., 2005). Focusing on rare species can offer insight into the factors driving rarity and model those species' presence accounting for the possibility that they are rare under specific conditions.

Finally, sampling protocols might affect the perception of rarity (Arscott et al., 2006). Incorporating rare species in bioassessment might also mean taking into account common species that were just not sampled at their true abundance with a specific sampling method, but do carry significant ecological information and react differently to ecosystem stress (Poos & Jackson, 2012).

1.4.3 Monitoring alien taxa

Monitoring might focus on communities, but it can also focus on individual species. In the case of alien/invasive species, early detection, while they are still rare, can be critical for native ecosystems (Guareschi et al., 2017). Monitoring methods should also cover those rare taxa, as regular protocols might simply miss them and falsely register them as absent (Jerde et al., 2011). In conjunction with the rare native species' higher risk potential under environmental change, unique niches might become available, rendering those ecosystems more susceptible to invasions (Alther et al., 2019; Lyons & Schwartz, 2001).

1.4.4 Conservation

When designing conservation policies and measures, rarity and endangerment often drive the distribution of resources and establishment of biodiversity conservation areas

(Gaston, 1994; Neeson et al., 2018), because of rare species assumed higher extinction potential (Cunningham & Lindenmayer, 2005). Confirming their presence in an area can be a strong argument in support of management actions (Lenat & Resh, 2001; Venette et al., 2002). However, the different approach to rare species from species and ecosystem conservation perspectives can lead to conflicting priorities when establishing such projects. Albuquerque & Beier (2015) suggested weighing species based on their rarity and ranking prospective conservation land sites based on their rarity weight, to estimate the maximum number of species that can be protected in a given number of sites or the minimum number of sites required to protect a given number of species. But Neeson et al. (2018) showed that maximum habitat area protection criteria mostly benefit common species.

In the absence of one universal explanation for the phenomenon of rarity, the study of rare species can still reveal patterns to support the establishment of effective conservation measures (Spitale, 2012). If the goal is the maximization of protected species richness, common and rare species could be weighted equally. The latter will still constitute a larger part of the conservation goal than the former (Lennon et al., 2004), while the former will also be included in the conservation prioritization. Conservation of rare species can also have economic benefits, with rare species given higher value from a human perspective, after they are acknowledged as rare, for the ecosystem services they provide (see section 1.3.2). A negative side-effect of this might be that along with this value, exploitation of them may accelerate extinction (Courchamp et al., 2006).

1.4.5 Dispersal

The ecosystems of monitoring or conservation interest can form networks of connected areas, each hosting its own species pool. Local populations appearing to survive in the

long term at low densities might be sustained by an influx of migrating individuals from source populations (Vermeij & Grosberg, 2018). The scale of a study can influence the observed patterns. Multiscale studies can assist decision making for predicting extinction risk of rare species, even though in general invertebrate studies focus on a single scale (Leroy et al., 2013). Such cases should assist conservation strategies to devise plans to conserve either the network in its entirety, or at least the source populations.

1.4.6 Ecosystem function

Rare species can have distinctive combinations of functional traits and thus constitute important contributors to the functional diversity of the ecosystem (Mouillot et al., 2013) and even perform the role of keystone species for their ecosystems (Bond, 1994). It is common to assume a correlation between species abundance or biomass and functional contribution, rendering rare species unimportant (Dee et al., 2019). But rare species' functional profiles might also support the community against adverse changes, increasing its functional breadth if they are complementary to the common species' profiles, or by offering alternative community structure that will perform the same ecosystem function in case of redundant functional profiles (Daam et al., 2019; Winfree et al., 2015).

1.4.7 Taxonomy

The decline in taxonomic knowledge and numbers of active taxonomists is well known (Hopkins & Freckleton, 2002). Such a trend can lead to a reduction in the level of available information, which will in turn lead to problems in monitoring, conservation and basic ecological studies. Detailed study and understanding of rarity require a fine level of taxonomy, which is not always available (Arscott et al., 2006). The need to study rare species can be an incentive for more detailed taxonomic work, which in turn will allow better incorporation of rare species in ecological studies. One could argue that with

the advance of molecular tools, morphology-based taxonomy will soon be obsolete, but we are still far from using molecular tools for every-day conservation projects. Even then, communication and understanding of natural patterns will always be easier when related to a certain picture of a species, carrying a certain name. And equally important, scientific results will need to be accessible and comprehensible by non-scientific audience.

1.4.8 Evolution

The study of rare species can also shed light onto the potential evolutionary advantage of rarity as a condition under which species' attributes might be advantageous in an evolutionary context, remaining rare over evolutionary time (Vermeij & Grosberg, 2018). Evolutionary established, specialised predator-prey relationships or consumer-dietary resource relationships might be hindered by the rarity of the food resource, and thus render rarity an advantage.

1.4.9 Innate value – Bioprospecting

Finally, just like every species on the planet, rare species deserve attention in a research context and conservation whether or not they are considered "important" under any given criteria. Additionally, bioprospecting, i.e. potential future contributions, suggests species might have resources and services to offer still unknown. To reveal them, our focus should also turn to the rare species that often remain marginalized in species-specific studies (Dee et al., 2019).

1.5 Problems caused by the rare species

1.5.1 Sampling, sorting and identification

Obstacles set by rare species during sampling and sample processing relate largely to the greater effort and cost required to study them or even simply include them in community

analyses. As the species-area relationship predicts, more or bigger samples will give larger numbers of species and individuals. However, at low abundances, rare species are difficult to sample in a standardized way, if at all (Reddin et al., 2015; Vermeij & Grosberg, 2018).

Traditional freshwater macroinvertebrate community studies collect three to five replicates, aiming to describe the community rather than collect specific species. In comparison to other community types this might be considered overly low, and it can miss rare species, effectively excluding them from the samples (Cao et al., 1998). Such incomplete samples might miss the full extent of differences between sites (Cao et al., 1998). On the other hand, the sampling effort required to assemble a species list that is representative of reality can increase to unrealistic levels in some diverse communities (Cao, Williams, et al., 1997). Some of the rare species might just be vagrants, stochastically drifting into the sampled habitat (Cao et al., 2001). They would not normally occupy that habitat and their presence might confound the results. It depends on the study aim, whether rare species need to be sampled and accounted for. Species richness or functional diversity estimations require higher sampling effort, as they depend on the rare species or rare functional trait combinations, in comparison to, for example, studies on beta diversity (Sgarbi et al., 2020).

The use of rare species can also be prevented by the level of taxa identification. Understanding patterns of rarity requires the finest level of taxonomy (Arscott et al., 2006). Species level identification might require the services of taxonomy experts and even then, there might be species still undescribed (Dudgeon et al., 2006). This is often the case for plant or invertebrate taxonomic groups and/or areas without a long history of taxonomic work. Very young individuals (e.g. early instar insect larvae) of different species might be indistinguishable from each other (Joy & Death, 2013; Winterbourn et

al., 2006). All these factors, during sampling, processing or identifying the samples might increase the required time and expertise and consequently the cost of a study (Faith & Norris, 1989).

1.5.2 Analysis

Rare species in communities can create problems for statistical analysis. The development and use of theories or models on assemblages with many rare species (as are most invertebrate assemblages) might be hindered by a lack of knowledge of these species' characteristics (Leroy et al., 2013). Species distribution modeling can be affected by the excessive number of zeros in rare species data (resulting in data overdispersion) and require specific modeling approaches (Blasco-Moreno et al., 2019; Lennon et al., 2004) and sparse community matrices (Gauch & Gauch, 1982). In those multivariate analyses that require data normality, it is unlikely to be satisfied by potentially zero-inflated, overdispersed data (Clarke & Green, 1988). Rare species might be ecological outliers in their communities, found in the margins of their niche breadth, even unable to reproduce, confounding studies on niche characteristics (Gaston, 1994) and species association (Gauch & Gauch, 1982). Furthermore, the inherent characteristics of rarity can differ radically among species. The lack of a single way to define rare species results in a lack of a single way to distinguish them from common ones (Gaston, 1994), and a lack of a single way to respond to their presence in samples. Drivers of rarity might need to be distinguished on a case by case and species by species basis, as some might be rare due to human impacts, and others naturally rare (Vermeij & Grosberg, 2018).

1.5.3 Results interpretation/Information content

Rare species are often considered statistically noisy, not showing clear patterns, obstructing the differentiation between different assemblages (Reddin et al., 2015) and not offering meaningful classifications of ecosystems (Marchant, 2002), while only providing redundant information and adding only little additional value to studies (Marchant, 1999; McCune et al., 2004). Lennon et al. (2004) in their study on birds suggested that "common species are commoner than rare species are rare", meaning that common species are more often common and informative of species richness patterns than rare species, which are not as often present in their low abundances and cannot reliably indicate high richness patterns. Winfree et al. (2015) focused on ecosystem function and services and suggested that abundance fluctuations affected ecosystem services more than species richness fluctuations and thus common species were more important than rare ones.

Rarity patterns can change with scale (Hartley & Kunin, 2003), hindering the clarification of their effect on community structure analyses. Relative information content of rare species might also differ among taxonomic groups. In freshwater macroinvertebrates the relationship between communities and their environment has been found to follow the same patterns for different taxonomic levels (Heino, 2008), rendering species level identification unnecessary, as higher taxonomic level datasets may provide the same amount of information. But in the case of rare freshwater fish, Poos & Jackson (2012) found that the inclusion or exclusion of rare species affected bioassessment.

Whether rare taxa are useful in bioassessment will also depend on the effect and changes one wishes to assess. Natural, overarching environmental gradients such as climate and geology can usually be characterized just by the common species, with no need for rare species to be considered. However, human-induced changes are unlikely to

override such massive environmental factors, and more importantly bioassessment aims to detect relevant biological changes at an early stage, thus relying on rare species.

1.5.4 Conservation

Conservation actions require a good knowledge of the natural history of the species in focus. In diverse communities, e.g. freshwater ecosystems, this can be particularly difficult as most species will be rare (Dudgeon et al., 2006). Ineffective sampling methods can affect whether species of conservation concern will qualify for set criteria (Queheillalt et al., 2002). Different monitoring methods might be required to cover both common and rare species (Pearman & Weber, 2007). While anyone will acknowledge the need for conservation actions taken in favour of rare species, such a focus might disregard the needs of common species, despite a global trend of common species declining faster than rare ones (Neeson et al., 2018). Even when aiming for networks of areas covering distributions of both common and rare species, rare species are unlikely to be covered by the most cost-effective plan (Neeson et al., 2018).

Leroy et al. (2012) argued against the inclusion of vagrant/rare species in community studies on the grounds that conserving them in an ecosystem where they are only occasionally or stochastically found, is a waste of funds. But apart from the inherent difficulty of distinguishing a rare resident from a vagrant species, if they are not consistently found in a specific ecosystem – and normally do not have the potential to establish in it at the local commoner species' expense, as invasive species would do – then they are not very likely to take advantage of conservation actions carried out.

1.6 Attitudes towards rare species in freshwater studies

1.6.1 Sampling – Sorting – Identification

1.6.1.1 Reasons for excluding rare species

Sampling protocols can have significant impact on a community's perceived structure; method, timing, effort (i.e. the number of replicates or the size of samples) will affect both the common and rare assemblages. For strong gradients where clear differences are expected, a coarse taxonomic resolution (e.g. family) and/or subsampling can be enough and more cost effective (Arscott et al., 2006).

Marchant (1999) claimed that 200-300 individuals are enough for stream bioassessment, will allow for precise multivariate classification of the sites and will provide sufficient data for predictive modeling. Sgarbi et al. (2020) also suggested setting a number of counted individuals for a given species, allowing for more samples with lower sampling effort per sample. In their study, the remaining assemblages showed moderate to high correlation with the complete assemblages even when 95% of the individuals were removed. Counting specific numbers of individuals for a given species would still require all individuals to be assessed but would give more accurate richness estimates (Sgarbi et al., 2020). A potential caveat with their study is that the identification was at the genus level, already pooling common and rare species. But similar patterns were observed in less genera rich Finnish streams (Heino, 2008). In Aotearoa New Zealand, Stark et al. (2001) suggested 200 individuals and a scan for rare taxa for biomonitoring purposes, while Duggan et al. (2002) suggested 100 individuals would suffice to assess biometric indices. However, this method can be biased towards large rare taxa. Small individuals will be more difficult to find and designate as rare, as they will require identification under the stereoscope. Relative rarity in such diverse communities depends on the total abundance in the sample. Apart from a rough

differentiation between common and rare taxa, this protocol will give rather unstandardized results depending on the experience of the collector and the actual sizes of the rare taxa. Only higher-level identification will be possible in most cases and all individuals will need to be assessed to determine taxon rarity.

1.6.1.2 Reasons for retaining rare species

Quantification of rare species is influenced by the few, overly abundant species (Arscott et al., 2006). Cao et al. (2001) suggested extensive qualitative sampling instead of more fund- and effort-demanding quantitative sampling (Leroy et al., 2012), on the grounds that most information is retained in the community's composition, not structure. If communities' differences are expected to be subtle or related to multiple stressors, then the most accurate composition should be recorded (Arscott et al., 2006; Cao et al., 1998). Doberstein et al. (2000) also found arguments in favour of subsampling invalid. Maintaining all species in an analysis reduces variability in diversity indices and distinguishes more accurately between stream quality classes (Doberstein et al., 2000).

To maximise the list of species sampled in a site, additional methodologies have been suggested to replace or, more usually, support the benthic samples. For example, flying adult aquatic insects can offer a finer taxonomic resolution (Joy & Death, 2013), and molecular tools, such as (e)DNA metabarcoding, can also offer finer taxonomic resolution while coming from the same benthic samples (Elbrecht et al., 2017; Elbrecht & Leese, 2015).

1.6.2 Data processing

1.6.2.1 Reasons for excluding rare species

The “rare species treatment” often takes place just before the analysis (Arscott et al., 2006). Rare taxa that have been collected, identified and recorded, are removed from the datasets. Formerly, this reduced computing time and storage space (Gauch & Gauch, 1982), but now such an advantage is obsolete (Cao et al., 2001). Stream ecosystems are very dynamic. Using all species in the dataset can produce low similarity results even among samples that would not be expected to differ, e.g. from the same site over time or from sites within a uniform stream segment (Lenat & Resh, 2001). This noise might mask existing relationships between species and their environment (Arscott et al., 2006). Removing stochastic outliers and taxonomic errors, a more cohesive dataset might offer clearer and more easily interpretable results (Arscott et al., 2006; Lenat & Resh, 2001). Nevertheless, distinguishing such “accidental” rare species from resident rare species is unlikely.

Raising the taxonomic level might reduce the rare species “noise”, by grouping them with congeneric or confamiliar species that might respond similarly to the environment (Heino, 2008). But this data-treatment can be problematic. As Hawkins et al. (2000) and Heino (2005) highlight, congeneric species in rich communities might have different niches because of adaptive radiation. And if rare species occupy similar niches to their abundant congenerics, the presumed noise should not be so prevalent as to obstruct pattern evaluation.

There is a wide range of filtering criteria used to exclude rare taxa. Usually, they incorporate one or more axes of Rabinowitz's (1981) rarity typology, i.e. abundance, distribution or habitat specificity. Relative abundance criteria might range from 0.05% to 1 or 2% of the total abundance or the abundance of the most abundant taxon, in a site or

over the whole study area (Table 1.2). It is highly unlikely that all species in an assemblage will directly interact with each other, so that their relative abundances will carry meaningful information. In very diverse communities such as freshwater macroinvertebrates, high cut-off limits such as 5% will render almost all species rare. Their removal will lead to species poor assemblages, responsive only to very strong gradients. Marchant (2002), argued against incorporating rare species in analyses, suggesting that if bioassessment is unable to detect change through common species, then the method is flawed. But while he showed this for subtle gradients, he did not address the effect of study scale (Cao et al., 2001). On the other hand, as Cao et al. (1998) suggested, bioassessment methods that get negatively affected by rare species, might not be suitable either.

Other cut-off limits are based on absolute abundance. Singletons and doubletons (species represented by one or two individuals respectively) might be eliminated as potential vagrant species or identification errors. But these groups might be used by richness estimators (e.g. Chao1, Chao2 species richness estimator – Chao et al., 2005). For these reasons Colwell (2013) suggested 10 individuals within a taxon. Cao et al. (1997) assessed the effect of rare species deletion, setting the limit at 1, 5, 10 and 18 individuals in Aufwuchs colonization samples. The effect depended on the cut-off limit, sample size and statistical methods, with the lower limits, unsurprisingly, having a smaller effect. However, the sampling method will affect the rare species assemblage. Passive colonization samples will collect very different assemblages from active sampling methods, such as kick-nets or Surber samplers.

Distribution or occupancy criteria are also used to define rare species (Table 1.2), by setting the absolute or relative number of sampled sites where a species is present in an area (Quinn & Hickey, 1990a). Cao et al. (1998) assessed the effect of deleting species

present in up to 1, 2 and 5 sites. As expected, the higher the number of sites set as a criterion, the larger the effect on species richness. However, with occupancy percentage criteria, there is usually a minimum possible percentage that can be set as a cut-off point, which is determined by the total number of sites in the study. For example, with a 20-site study, the minimum percentage of occupancy for a species to be considered rare is 5%, as that is one site.

Table 1.2: Rarity criteria employed in freshwater ecology studies, which assessed the effect of retaining and excluding rare taxa from datasets to reveal natural community patterns, excluded rare taxa to reduce statistical noise without assessing the validity of this action, or focused only on the rare components of freshwater communities without assessing the effect of their exclusion or retention. Spatial criteria defined rare taxa based on absolute/relative occurrences across a study area. Temporal criteria defined rare taxa based on absolute/relative occurrence frequency during a study period. Abundance criteria defined rare taxa based on absolute/ relative abundance with regards to the most abundant taxon or the total abundance, in their respective samples or over the whole study. Occurrence probability defined rare taxa based on their modelled probability to be collected at a site. Numbers correspond to the list of references.

Action / Criteria	Proposed retention of rare taxa	Proposed exclusion of rare taxa	Exclusion of rare taxa without supporting analysis	Studies focused only on rare taxa
Spatial	13, 82, 123, 179, 226, 239	140, 148, 173, 244, 262	174, 202, 205, 206, 219, 247, 256, 282, 324	8, 151, 188, 209, 210, 223, 227, 266, 269, 289
Temporal	13, 260		69	254, 269
Abundance	13, 50, 51, 99, 109, 123, 131, 178, 226, 260, 344	140, 244, 276, 344	180, 207, 208, 219, 271, 282, 338, 342	8, 16, 95, 151, 277, 280, 299
Occurrence probability	74, 179, 316	12, 67, 231, 320	46, 169	

1.6.2.2 Reasons for retaining rare species

If the study focuses on a small area, where common species are expected to be abundant everywhere and the environmental gradients are not particularly strong, common taxa are

less likely to offer significant distinguishing power. In such cases the common taxa can be removed and the rare used instead (Cao et al., 2001). Hawkins et al. (2000) deleted the species that were present in > 95% of the sites to improve their models' stream site classification. Overly abundant taxa (e.g. chironomids & oligochaetes), might also mask rare species' patterns without offering greater distinguishing power than less common ones (Cao, Williams, et al., 1997), or obscure the distinction between human impacts and natural variation (Jiang et al., 2014).

1.6.3 Analysis

1.6.3.1 Reasons for excluding rare species

Whether to include rare species in the analysis or not depends on the study question and the statistical methods. Marchant (1999) argued that the common transformation of community abundance data, log(x+1), already increases the weight of rare species (Clarke & Green, 1988), invalidating the claim that statistical analysis favors common species (Cao et al., 1998). Marchant (1999) also suggested that the bulk of the information lies in the species list instead of the community's structure and thus special focus on the rare species because of their low abundance is unjustifiable.

Some community similarity measures overweight rare species (e.g. Canberra metric, Jaccard index), and their exclusion might be a valid data processing decision, while others (e.g. Bray-Curtis index) overweight abundant species and for them rare species deletion will make no difference (Cao, Williams, et al., 1997). Indirect rare species exclusion in bioassessment via fixed-count subsampling can also benefit univariate (Yu et al., 2017), multimetric and O/E indices (Chen et al., 2015).

1.6.3.2 Reasons for retaining rare species

Rare species in multivariate analyses can distinguish outlying communities (Cao et al., 2001) and provide site-specific information (Poos & Jackson, 2012). Fore et al. (1996) argued that deleting rare species is an example of statistics overshadowing biological common sense. Despite potential zero-inflation, rare species' datasets contain information and can indicate species-rich, diverse and possibly pristine communities (Fore et al., 1996; Thorne et al., 1999). Temporal change of community structure will depend more on species turnover than species loss (Sgarbi et al., 2020), rendering a comprehensive species list highly important. If most information lies within the list of species in a community instead of their abundances (Marchant, 1999), the inclusion of rare species is even more necessary, as they comprise the biggest part of the community's species pool (Cao & Williams, 1999). Species-poor communities are less likely to be heavily affected by rare species' deletion than species-rich ones. Consequently, comparison of species richness between species-rich and poor communities will be biased in favor of the latter (Cao et al., 1998).

Classic hypothesis testing and requirements for multivariate normality are no longer considered necessary for ecological research. Ordination and clustering analyses are more commonly used, releasing analyses from such prerequisites, and can incorporate rare species (Cao et al., 2001; Clarke & Green, 1988). Analyses might employ various transformations on raw abundance data, such as Hellinger, square root, fourth root, log(x+1) transformation, or presence-absence in order to reduce the impact of either component (Poos & Jackson, 2012). Finally, biomonitoring and conservation programs, such as the System for Evaluating Rivers for Conservation (SERCON, Boon et al., 2002, 1994), or the use of indices, such as the Biological Monitoring Working Party (ISO-

BMWP, 1979) might be improved in terms of accuracy by the inclusion of rare species (Yu et al., 2017).

1.7 Comparison between total and common assemblages

1.7.1 Reasons for excluding rare species

Sgarbi et al. (2020) evaluated the effect of rare and common species deletion in ordinations. Common species ordinations resembled complete communities more in comparison to the rare assemblages, but no difference was observed with presence-absence data. This is surprising, as the largest amount of information is presumed to be contained in the list of species present in a community instead of their abundance (Marchant, 1999), and the largest component of species richness comprises rare species. Their high variability might have been a stronger driver for their ordination patterns. Heino & Soininen (2010) did not find significant contribution of rare species to turnover in metacommunities, based on limited distribution as a rarity proxy. But groups so different in their ecology, community structure and dispersal as diatoms, macroinvertebrates and plankton may not be affected by the same drivers in a metacommunity context. Quinlan & Smol (2001) used Chironomids from subfossil samples as paleoindicators. Despite using untransformed abundance data, moderate deletion of rare species improved their models. The fact that rare species' raw abundance data can obscure natural patterns, could indicate that they comprise an overly variable but significant part of community structure. Their inclusion in analyses would require data processing to deal with increased variability.

Yu et al. (2017) assessed the effect of rare taxa exclusion on several biotic indices. The result depended on the characteristics of each index. Indices weighting common

species (e.g. Simpson's index) were not heavily affected by rare taxa exclusion, contrasting indices closer to taxa richness (e.g. BMWP index).

Hawkins et al. (2000) and Ostermiller & Hawkins (2004) found that their biomonitoring models were more robust after omitting rare species. Hawkins et al. (2000) noted the greater standard deviation of the complete dataset's O/E values compared to the lower and more consistent values of the reduced dataset, but did not assess whether this pattern was related to the higher variability of rare taxa or rarity per se. Van Sickle et al. (2007), in a larger scale study found similar results. They suggested that rare taxa appeared unreliable for quantitative bioassessment because of their unpredictability and variability but can offer qualitative information. Aroviita et al. (2010) also did not consider rare species necessary to accurately evaluate a stream ecosystem's condition. Reduced datasets sufficiently indicated needs for management of streams hosting threatened species. However, greater accuracy could be achieved with a more representative spatiotemporal study design and the inclusion of rare species can indicate biodiversity hotspots. Chen et al. (2015) agreed that rare taxa contributed mostly to higher variability. Their suggestion for subsampling of 500 individuals (in contrast to 300-350 individuals by Ostermiller & Hawkins (2004) and Van Sickle et al. (2007)) will lead to greater species richness and higher numbers of rare taxa.

1.7.2 Reasons for retaining rare species

Faith & Norris (1989) found more and stronger relationships between water chemistry variables and community structure when the rare species were retained. However, they could not clarify whether their results were a product of the addition of more or specifically rare species, which might also be related to statistical noise (Faith & Norris, 1989). Robinson et al. (2000) found rare macroinvertebrates to be important for

evaluating stream condition on a temporal scale. A shift in species' frequencies with time might indicate a system that is naturally variable, under disturbance or recovering post-disturbance. However, a disturbance acting on common species might be revealed with the exclusion of the rare ones, confirming the multi-faceted element of rarity. Cucherousset et al. (2008) found common species to follow species richness patterns better than rare ones. The abundance distribution with a few common and many rare species was not observed in their study, possibly because of their rarity definition and/or that the three biogeographical regions comprising their sampling area contributed different common species. However, on a species-by-species basis, the information content of the rare species correlated more strongly with the richness patterns. Hence, they concluded that none of the two components can be safely considered to cover all richness patterns.

Doberstein et al. (2000) compared subsamples with fully enumerated samples and found subsamples to be more variable and statistically weaker. Lost information led to fine differences remaining hidden and only very different groups being distinguishable. Turak & Koop (2003) showed that detection of low impacts requires rare taxa. Common taxa might be widespread and resistant to low level disturbance, hence not indicating disturbance. However, Turak & Koop (2003) used mostly family-level taxonomy. Rare families are more likely to differ from common ones than rare species from congeneric common ones. When rare species are pooled into higher taxonomic levels (e.g. family), their relationships with their environment might be masked by their abundant confamiliars. Nijboer & Verdonschot (2004) suggested that excluding rare taxa, whether scarce or narrowly distributed, misjudges stream health. Interestingly, narrowly distributed taxa were related to healthy streams, while scarce taxa were related to degraded streams. Mean abundance per sample is not often used as a rarity definition in

freshwater studies, but there is no indication other definitions would give very different results. Arscott et al. (2006) did not find significant differences in ordinations or environmental drivers whether they included or excluded rare taxa. Common taxa even contributed noisy information. Absence of difference could indicate rare taxa redundancy, but while the relative difference between species richness in impacted and unimpacted sites remained the same, the actual difference was reduced when the rare taxa were excluded, underestimating the true impact. Guareschi et al. (2017) found significant effects of rare taxa exclusion on single and multimetric macroinvertebrate-based indices. They used family abundances and a low rarity cut-off point at three individuals, which could be expected to only exclude individuals that stochastically drifted in the samples. Yet the effect was significant, supporting the inclusion of rare taxa in bioassessement, depending on the metric (Guareschi et al., 2017; Yu et al., 2017).

Clarke & Murphy (2006) distinguished O/E estimates from reference and impacted sites. Rare taxa deletion gave more variable results for impacted sites, and less variable for reference sites. Their disagreement with other similar studies (Hawkins et al., 2000; Ostermiller & Hawkins, 2004) was attributed to the sampling method and sample processing protocol, showcasing the effect that every step of the procedure can have on the conclusions.

1.8 Conclusions

Rarity is a complex concept. There cannot be a universal definition; different communities follow different patterns. Comparisons of different studies or the joint analysis of different groups of organisms can be particularly difficult. How rare species will be defined and whether they will be excluded from a study or not, ultimately depends on the research question and the sampling and analytical tools the researcher wishes to

use. Rare species are often considered noisy or redundant and are excluded from samples and/or analyses to reduce costs and/or increase the analytical precision. Nevertheless, most studies do acknowledge rare species deserve attention and conservation, while species population trends might be detected from data collected for other purposes, such as biomonitoring.

To determine which factors govern freshwater macroinvertebrate rarity, comparisons should be made between communities sampled with the same method, following the same protocols, in similar types of streams and basins, across latitudes and across different study scales. Different definitions of rarity could then be applied and the existence of natural patterns investigated.

Species level identification of benthic macroinvertebrates is not always possible; adult aquatic insects can provide an additional component that could support benthic macroinvertebrate diversity studies (Joy & Death, 2013). Even though living out of the water, adult aquatic insects are inextricably connected to freshwater habitats for feeding, mating and egg laying and respond to similar environmental changes (Collier et al., 1997). They have been studied for longer and have been described in greater detail in comparison to their larval stages (Smith, 2014). In most cases, it is relatively easy to identify the species of a male individual based on its genitalia and the female individuals at least to genus level. Consequently, they can offer a more complete species list to freshwater studies.

New approaches will pose additional questions about the structure of the community, the way it responds to different sampling methods, environmental change etc. It is unlikely that there will be one method that will give a definitive answer to every question related to rare species, from the sampling stage until the interpretation of the analysis results. The best approach seems to be to take into account the different factors

that can affect observed patterns of rarity and attempt to disentangle their contributions to them.

Aotearoa New Zealand streams are characterized by steep slopes and frequent floods, removing organisms and materials downstream (Winterbourn et al., 1981). Benthic macroinvertebrates are characterized by high endemicity and low numbers of invasive species (Boothroyd, 2000; Winterbourn, 2004). They are more flexible in their life-cycle's periodicity, less synchronized, and with longer flying and egg-hatching periods (Scarsbrook, 2000). The threats that native invertebrates face are water abstraction for industrial, agricultural and domestic use, flow changes, invasive species, channelization, sedimentation, eutrophication, riparian land-use change, climate change, and of the highest stresses, agricultural intensification. Taxonomic knowledge for Aotearoa New Zealand species still remains incomplete. Many species that are rare in terms of abundance or distribution range, are likely to be found in similarly rare or highly specialised habitats that are not regularly monitored, but are also threatened (Joy & Death, 2013).

1.9 Thesis structure and aims

This thesis attempts to fill parts of the knowledge gap surrounding rare stream macroinvertebrates in Aotearoa New Zealand. I examine whether the rare taxa components of lotic macroinvertebrate communities are related to their environment in the same way as the common taxa components, and whether the inclusion or exclusion of rare taxa affects the assessment of the complete community. I examine linkages between rarity definition and biodiversity, biomonitoring, sampling method selection, local environment drivers, network position and dispersal. The objectives of the chapters are as follows:

- **Chapter 2** examines the effect that rare species deletion has on stream biomonitoring. Rare taxa deletion is a data treatment often applied in international literature, aspiring to clarify ecological patterns. I apply several rarity definitions on communities along an organic pollution gradient in streams across the two main Islands of Aotearoa New Zealand, and delete the rare components to assess the effect this action has on biomonitoring metrics, such as the Macroinvertebrate Community Index (MCI) and its quantitative variant (QMCI), and regressions of these metrics with nutrient concentrations.
- **Chapter 3** examines the effect of sampling method and life stage on describing biodiversity patterns of Trichoptera assemblages and their rare components, in pristine, mountainous streams in the central North Island of Aotearoa New Zealand. I assess biodiversity patterns in Trichoptera assemblages and their rare components, collected by two benthic sampling methods (kick-net and Surbers) and two adult trapping methods (UV-light traps and Sea-Land-Air-Malaise traps). In this and the following Chapters I define rare taxa based on their relative abundance in each site, to ensure increased detail in distinguishing the assemblage of taxa not reaching high abundances under local conditions.
- **Chapter 4** examines whether the structure of aquatic macroinvertebrate communities from pristine, mountainous streams, and their common and rare components, are driven by the same local scale environmental factors. It also assesses whether the life stage of the aquatic insects, benthic larvae or flying adults, affects the relationship of the communities and their common and rare components with their local environment.
- **Chapter 5** examines the effect that the position within the stream network and the dispersal mode have on biodiversity patterns of common and rare benthic

macroinvertebrates and the drivers of assemblage structur, both local (environmental) and dispersal related. I use benthic communities from three drainage basins of the central North Island of Aotearoa New Zealand. Two stream network positions are examined (headwaters and mainstems) and three modes of dispersal (aquatic passive dispersers, and flying passive and active dispersers).

- **Chapter 6** synthesizes the knowledge gained from the previous chapters of the thesis.

Chapter 2

Effect of rare taxa on bioassessment using stream invertebrates.

Abstract

A large percentage of species richness in natural communities comprises rare taxa. These are often considered noisy and redundant to data analysis and are thus often excluded from ecological studies. We assessed the effect of these exclusions on biomonitoring of stream macroinvertebrates in Aotearoa New Zealand. We used macroinvertebrate data from 64 streams and rivers around the country, collected in 2005 as part of the National River Water Quality Network. We excluded rare taxa based on both site-specific and study-wide criteria, that set limits for inclusion of taxa based on the absolute and relative abundance, occurrence frequency, subsamples and species abundance ranking. The Macroinvertebrate Community Index was heavily affected, misclassifying numerous streams, upgrading the water quality classification for some and downgrading it for others. The biggest changes occurred using relative abundance criteria, which retained only a few, very abundant and tolerant taxa, downgrading the average index value for excellent, good and fair quality sites. The Quantitative MCI was not affected much, because of its numerical basis. In general, community structure correlated strongly between assemblages with different types of rare taxa excluded. The community structure of the quality class groups defined by each index were clearly distinguished after rare taxa exclusion, apart from some site-specific criteria. The relationship between MCI and nutrient concentrations (NOx and DRP) was weakened by extensive rare taxa exclusion. Study-wide relative abundance criteria excluded rare sensitive taxa, which could act as early warning indicators of increasing enrichment. The QMCI-nutrient relationship was not affected. The exclusion of rare taxa did not offer any significant advantages to biomonitoring and instead often led to misclassifications of the ecological quality of streams, with potentially severe implications for the distribution of management and restoration funds.

2.1 Introduction

Freshwater ecosystems are among the most threatened in the world (Dudgeon et al., 2006; Reid et al., 2018). Despite covering less than 1% of the planet, they host a disproportionately rich biodiversity that is declining faster than in terrestrial ecosystems, (Gleick, 1993; Sala et al., 2000). Major threats to their biota include overexploitation, water pollution, flow modification, habitat degradation, alien species invasion and climate change (Dudgeon et al., 2006; Reid et al., 2018).

The fauna in freshwater ecosystems in Aotearoa New Zealand are characterized by a high degree of endemicity and are threatened by agricultural intensification, urbanization, invasive species and climate change (Joy & Death, 2013). Water quality assessed at National River Water Quality Network (NRWQN) monitoring sites has been declining rapidly since 1989 because of intensification of livestock farming (Ballantine & Davies-Colley, 2010), 74% of native fish are threatened or at risk (Weeks et al., 2016), and more than 50% of macroinvertebrate species are either threatened or data deficient (Boothroyd, 2000; Grainger et al., 2018).

In Aotearoa New Zealand, there is not a single overarching stream monitoring program (Buss et al., 2015). The National Institute of Water and Atmospheric research (NIWA) has 77 monitoring stations around the country for the NRWQN (Smith & McBride, 1990), and all Regional Councils monitor freshwaters in their regions, using a variety of site selection criteria and sampling protocols (Buss et al., 2015; Stark et al., 2001; Stark & Maxted, 2007a). The NRWQN records core variables (e.g. conductivity, temperature, visual clarity, *E. coli* and several forms of nitrogen and phosphorus), benthic periphyton growth and benthic macroinvertebrates (Davies-Colley et al., 2011). Ecosystem monitoring based on macroinvertebrates usually employs biodiversity indices, such as Ephemeroptera-Plecoptera-Trichoptera (EPT) richness and the suite of

macroinvertebrate community indices developed by Stark (1985) including the Macroinvertebrate Community Index (MCI) and Quantitative (Q)MCI. These indices were developed to assess organic enrichment effects on stream ecosystems, assigning tolerance values to macroinvertebrate taxa, but have also been linked with other land-use pressure gradients (Dolédec et al., 2006; Quinn et al., 1997; Townsend et al., 1997; Young & Collier, 2009).

Stream macroinvertebrate communities, like all communities, comprise a few common species and many rare ones (Gaston, 1994; Lenat & Resh, 2001). But the definition of rarity depends on the research question (Venette et al., 2002). Rabinowitz (1981) distinguished seven forms of rarity by characterising a species based on its local population size, geographic range and habitat specificity. Factors that may render a species rare can range from dispersion and colonisation ability to habitat patch distribution, physicochemical habitat requirements and biotic interactions (Gaston, 1994; McCreadie & Adler, 2008). However, a species' rarity status can also change in space and time, when its relative abundance changes because of shifts in other species' abundances, and it can also be affected by the sampling protocol and timing, or even stochastic events, such as drift (Cao et al., 2001; Gaston, 1994).

Rare species are routinely excluded from multivariate community analyses on the grounds they contain redundant information and obscure patterns due to their high variability (Marchant, 1999, 2002; McCune et al., 2002; Van Sickle et al., 2007). Exclusion is implemented by subsampling, identification to higher taxonomic level, or setting absolute/relative abundance and occupancy limits (Nijboer & Schmidt-Kloiber, 2004; also Chapter 1). Such approaches have been criticised as a statistics-over-ecology prioritisation problem (Fore et al., 1996), that can miss subtle natural or impact gradients indicated by rare species, or waste time until they detect an impact affecting rare species

first (Cao et al., 2001; Sweeney et al., 2011). Rare species' small populations can also be more susceptible to disturbance and extinction than common ones' (Purvis et al., 2000).

Exclusion of rare species from index-based bioassessment is not common. When employed, it assumes changes in common species are the only indicator of an impact happening and/or that they react first (Cao & Williams, 1999). Studies on the effect of rare species' exclusion on stream bioassessment have shown that this depends on the definition of rarity and the ecological state of a site (Cao et al., 1998). Nijboer & Schmidt-Kloiber (2004) found that exclusion of range limited species led to more conservative assessments, as these species tend to be found in better quality sites. Exclusion of species with low abundance is likely to result in conclusions of better water quality, as these taxa will be rare in non-ideal sites. Subsampling can also underestimate the true loss of species richness (Cao & Hawkins, 2005). In modelling-based bioassessment, deletion of rare species at high occurrence probability thresholds is likely to weaken the model's capability of assessing the ecological condition of both high- and low-quality sites (Clarke & Murphy, 2006). However, exclusion based on low occurrence probability can improve inferences made from the model, making it less variable and more precise, especially for low quality sites (Clarke & Murphy, 2006; Hawkins et al., 2000; Van Sickle et al., 2007), while still protecting threatened species (Aroviita et al., 2010).

In Aotearoa New Zealand, subsampling of 200 individuals is often applied in samples with overly abundant communities and rare taxa that may be missed are included by a sample scan (Stark et al., 2001). However, this scan can be biased towards larger species, while at the same time many taxa are impossible to differentiate with the naked eye. Therefore, this protocol can miss taxa low in abundance that are indistinguishable from more abundant taxa. However, Stark (1985) found the MCI index was robust to deletion of the rarest taxa (one or two individuals in a sample).

While established sample processing protocols in New Zealand partly address the presence of rare taxa, the effect of their deletion on biomonitoring has not been well studied. Rare taxa are also often excluded when the focus is not on biomonitoring, but rather on e.g., multivariate analysis. Using macroinvertebrate data collected for the NRWQN, we excluded rare taxa based on a series of rarity definitions and evaluated the effect of the exclusion on biomonitoring indices and their relationships to anthropogenic stressors. We hypothesized that: H1) MCI band assignment will be affected more than QMCI because of the reliance of the first one on species richness and the second on species abundances; H2) Higher quality streams' assessment will be affected more than lower quality ones', as the more sensitive taxa are expected to be relatively rare even in pristine conditions; H3) Regression between MCI and nutrients will be more affected than that between QMCI and nutrients because on the MCI relying on species richness and the rare taxa being more closely linked to environmental stressors.

2.2 Methods

The NRWQN macroinvertebrate and water chemistry data are publicly available and can be found at: https://teamwork.niwa.co.nz/collector/pages.action?key=NEDA. The year 2005 was selected as a case study because of the more balanced distribution of sites across the four quality classes for both biomonitoring indices in comparison to the other years in the NRWQN database.

2.2.1 Macroinvertebrate samples

Macroinvertebrate samples were collected from 64 sites in 31 river systems on the two main islands of Aotearoa New Zealand during the late austral Summer and Autumn of 2005 (Fig. 2.1). They were part of the annual monitoring surveys for New Zealand's

National Rivers Water Quality Network (NRWQN, Smith & McBride, 1990), conducted by the National Institute of Water and Atmospheric research (NIWA). Site selection was based on criteria listed in Smith & McBride (1990) and covers streams ranging from relatively pristine, to ones affected by agriculture, exotic forestry, industry and urban development (Scarsbrook et al., 2000).

Sampling took place during baseflow conditions (flow < $flow_{median}$), at least four weeks after any high flow. In each site seven Surber samples were collected (0.1 m^2 and 250 μm mesh nets) from as many substrates as possible, disturbing the streambed to a depth of 10 cm. The seven replicates were pooled at each site and subsampling used to reduce processing time (Smith & Quinn, 1991). They were identified to the lowest taxonomic level required for bioassessment in New Zealand (mostly species or genus), using Winterbourn et al. (2006) (see Quinn & Hickey (1990a) for more details).

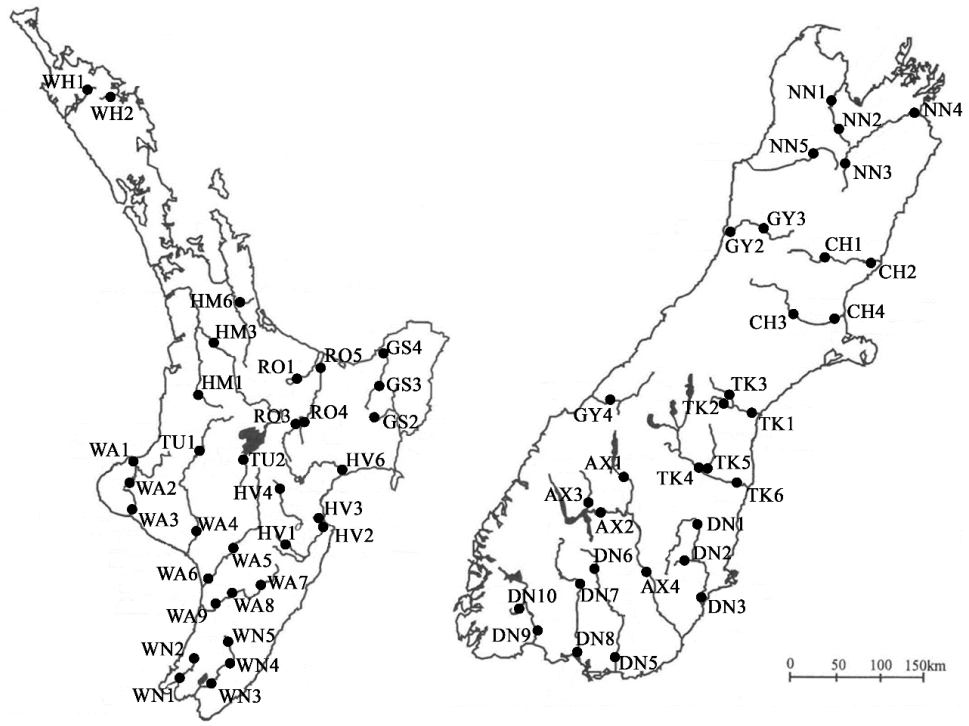

Figure 2.1: Macroinvertebrate sampling sites in New Zealand's National River Water Quality Network for the year 2005.

2.2.2 Rarity definitions

We defined the rare components in our dataset using several criteria found in the literature (Chapter 1), such as absolute and relative abundance (based on the total abundance of all taxa), applied on the community dataset of each site (site-specific criteria), on pooled communities from all sites (study-wide criteria), and occurrence frequency (Table 2.1). We deleted these components from the dataset and performed statistical analyses on the remaining common components. We also ranked the taxa according to their study-wide abundance and deleted the first quartile, i.e. 25 % of the least abundant taxa, following Gaston (1994). Finally, we simulated random subsampling of 200 individuals, as suggested by Stark et al. (2001) for monitoring New Zealand streams with numerous invertebrates (Protocol P2). We performed randomized subsampling 20 times and used the average abundances for multivariate analyses and the average biomonitoring indices for univariate analyses (see section 2.5).

Table 2.1: Rarity definitions used to distinguish rare and common taxa in the 64 NRWQN macroinvertebrate samples from streams and rivers across New Zealand, collected during the austral summer and autumn of 2005.

	In each sample	In the whole study
Absolute abundance	1 individual (singleton) – 2 individuals (doubleton) – 5 individuals – 10 individuals	
Relative abundance	0.1 % - 0.5 % - 1 % - 5 %	
Occurrence frequency	-	Unique (found in one site)
Subsample	200 individuals	-
Abundance ranking	-	First quartile of least abundant species

2.2.3 Bioassessment metrics

We calculated the Macroinvertebrate Community Index (MCI) and its quantitative variant (QMCI) for the complete dataset and excluding various rare taxa components as defined

above. The MCI uses presence-absence data, while the QMCI uses abundance data (Stark & Maxted, 2007b).

$$MCI = 20 * \frac{\sum_{i=1}^{S} a_i}{S}$$

where α_i = MCI tolerance score for the i^{th} taxon, and S = total number of taxa

$$QMCI = \frac{\sum_{i=1}^{S} n^i a^i}{N}$$

where n_i = number of individuals in the i^{th} taxon, a_i = MCI tolerance score for the i^{th} taxon, S = total number of taxa and N = total number of individuals

MCI values can range, in theory, between 0 and 200 (Stark, 1985), and QMCI values between 0 and 10 (Stark, 1998), with the higher values referring to more pristine conditions. In practice MCI usually ranges between 50 and 150 and QMCI between 2.5 and 7.5, with only extremely degraded streams reaching lower values (Stark & Maxted, 2007b). Both indices distinguish four quality classes; excellent, good, fair and poor (Stark & Maxted, 2007b). The National Policy Statement for Freshwater Management (NPS-FM – New Zealand Ministry for the Environment, 2020) defines the MCI and QMCI values for these categories (Table 2.2).

Table 2.2: Stream water quality classes based on the Macroinvertebrate Community Index (MCI) and Quantitative (Q)MCI, as defined in the National Policy Statement for Freshwater Management (New Zealand Ministry for the Environment, 2020)

Quality class	Description	MCI	QMCI
Excellent	Pristine conditions, almost no organic pollution or nutrient enrichment	≥130	≥6.5
Good	Mild organic pollution or nutrient enrichment	≥110 and <130	≥5.5 and <6.5
Fair	Moderate organic pollution or nutrient enrichment	≥90 and <110	≥4.5 and <5.5
	National bottom line	**90**	**4.5**
Poor	Severe organic pollution or nutrient enrichment	<90	<4.5

2.2.4 Nutrient measurements

Nitrogen and phosphorus are two nutrients commonly included, in various forms, in artificial fertilisers used in agriculture. The enrichment effect of their leaching from the ground into freshwater ecosystems has been well documented, boosting periphyton growth on the streambed and at high levels leading to eutrophication and algal blooms (Canning et al., 2021; Foote et al., 2015). In the New Zealand context, the MCI and QMCI were developed to assess organic pollution caused by increased nutrient inputs in lotic ecosystems (Stark, 1985). We used concentrations of Oxidised Nitrogen (Nitrite & Nitrate - NOx) and Dissolved Reactive Phosphorus (DRP) from 2004 as anthropogenic stressors affecting the macroinvertebrate communities of 2005. Two 1 L water samples were collected monthly from the sites, filled completely and transported in chilled, insulated, opaque containers to the NIWA-Hamilton laboratory overnight for analysis (Smith & McBride, 1990). They were analysed by a Lachat Flow Injection Analyser (Davies-Colley et al., 2011). We calculated the annual nutrient concentration medians for each site to assess their link to biological indices and macroinvertebrate communities under the differing rare taxa deletion criteria.

2.2.5 Data analysis

All analyses were run in R v.4.0.2 (R Core Team, 2020), except for the 2nd-stage multivariate analyses, which were run in PRIMER v.6 (Clarke & Gorley, 2006). In total we used 20 biotic matrices for the analyses; the complete matrix and 19 matrices with different rare components excluded.

After the exclusion of rare taxa, we recalculated the biomonitoring indices and reclassified water quality. We compared the frequency of sites that were designated to each quality class after excluding the rare taxa, to the original dataset with a Chi-square

analysis. To assess the effect of exclusion on streams with different water quality, we calculated the average MCI score of the taxa in the common and rare components that resulted from the application of the various rarity criteria on the full dataset. We then compared those means with t-test separately for each quality class defined by the MCI and the QMCI. Using Generalised Linear Models with Gaussian distributions, we compared the new index values to the original dataset for all 64 sites. Finally, we performed Pearson correlation between the original indices and the post-exclusion recalculated indices.

We examined community structure with the vegan package and log(x+1)-transformed abundance data. To examine whether the structure of communities belonging to the quality classes indicated by each index in the original dataset were similarly distinguished after the exclusion of rare taxa, we performed pairwise Permutational Analysis of Variance (PERMANOVA, Anderson, 2001). We used the RVAideMemoire package (Hervé, 2020), using 400 permutations, Bray-Curtis distances and Benjamini-Hochberg correction for type I errors (Benjamini & Hochberg, 1995). We performed non-metric multidimensional scaling (NMDS) with Bray-Curtis distances for each dataset and then 2nd stage NMDS to examine concordance between the matrices after the deletion of rare taxa (Clarke & Warwick, 2001). We produced a Spearman's rank correlation matrix among the resemblance matrices of the datasets with the 2ND STAGE routine in PRIMER and then performed the 2nd stage NMDS with the MDS routine.

To assess the strength of the relationship between the two nutrients and the multivariate community structure under different rare taxa definitions, we log(x+1) transformed the nutrient measurements and regressed them against the NMDS axes scores for each dataset. Similarly, we performed linear regression between the nutrients and the

MCI and QMCI indices for each dataset to assess the effect of rare taxa deletion on the relationship strength between bioassessment indices and potential stressors.

2.3 Results

In total 110 707 individuals from 76 taxa were collected in 64 streams and rivers in 2005, with richness ranging between five and 34 taxa (mean = 16).

In the original data, MCI indicated 8 sites were of excellent quality, 22 good, 27 fair and 7 poor. The wider site-specific rarity definitions significantly altered the classification ratios for both absolute (5 and 10 individuals) and relative abundance (1 and 5 %) criteria (Table 2.3). Numbers of sites at the ends of the quality gradient (excellent and poor) increased and the intermediate ones (good and fair) decreased (Fig. 2.2a). The largest effect was seen when taxa with ≤ 5 % of the total abundance in each site were excluded; 22 sites downgraded and 18 upgraded (Fig. 2.2b). The smallest difference occurred when taxa with ≤ 0.1 % of the total abundance were excluded; only 2 sites downgraded, and 3 sites upgraded. Study-wide criteria based on ranked and absolute abundance, and occurrence frequency excluded very few taxa, not affecting classification (Table 2.3). Relative abundance criteria lead to significant changes in site classification, downgrading 75 % of sites after deleting rare taxa with abundance ≤ 1 % of the total (Fig. 2.2b).

Table 2.3: Mean richness and abundance, and MCI and QMCI quality classification frequencies from stream macroinvertebrate communities and after the exclusion of rare taxa, along with Chi-square test significance of comparisons between the frequencies of the full dataset and after the exclusion of rare taxa Samples were collected in 64 streams and rivers during the austral summer and autumn of 2005 across New Zealand.

	Abundance	Richness	MCI					QMCI				
			Excellent	Good	Fair	Poor	X^2 sig.	Excellent	Good	Fair	Poor	X^2 sig.
Full dataset	110707	16.3	8	22	27	7		20	12	15	17	
singletons / sample	110482	12.8	9	22	24	9	0.818	19	13	14	18	0.97
doubletons / sample	110262	11.1	9	22	21	12	0.271	19	13	14	18	0.97
5 individuals / sample	109577	8.2	**16**	**18**	**16**	**14**	**0.001**	21	11	15	17	0.99
10 individuals / sample	108730	6.5	**13**	**13**	**23**	**14**	**0.006**	21	9	14	19	0.72
0.1 % / sample	110406	13.7	9	22	25	8	0.941	20	12	15	17	1.00
0.5 % / sample	109034	8.9	9	20	22	13	0.239	20	12	14	18	0.99
1 % / sample	107677	6.8	**11**	**15**	**22**	**16**	**0.016**	20	12	14	18	0.99
5% / sample	99805	3.4	**14**	**15**	**19**	**16**	**0.003**	21	10	14	19	0.87
200 subsample	11745	10.8	10	21	24	9	0.737	21	11	15	17	0.99
unique occurrence	110681	16.1	8	22	27	7	1.000	20	12	15	17	1.00
singletons overall	110702	16.2	8	22	27	7	1.000	20	12	15	17	1.00
doubletons overall	110694	16.1	8	22	27	7	1.000	20	12	15	17	1.00
5 individuals overall	110653	15.8	8	22	27	7	1.000	20	12	15	17	1.00
10 individuals overall	110627	15.6	8	22	27	7	1.000	20	12	15	17	1.00
0.1% overall	109750	12.7	8	20	27	9	0.886	20	12	14	18	0.99
0.5% overall	105462	8.3	**1**	**6**	**39**	**17**	**<0.001**	19	9	16	19	0.72
1% overall	102545	6.3	**1**	**3**	**23**	**36**	**<0.001**	18	9	16	20	0.63
5% overall	97646	5.4	**1**	**3**	**49**	**10**	**<0.001**	18	9	18	18	0.62
25% least abundant taxa	110658	15.9	8	22	27	7	1.000	20	12	15	17	1.00

Significance level: < 0.05

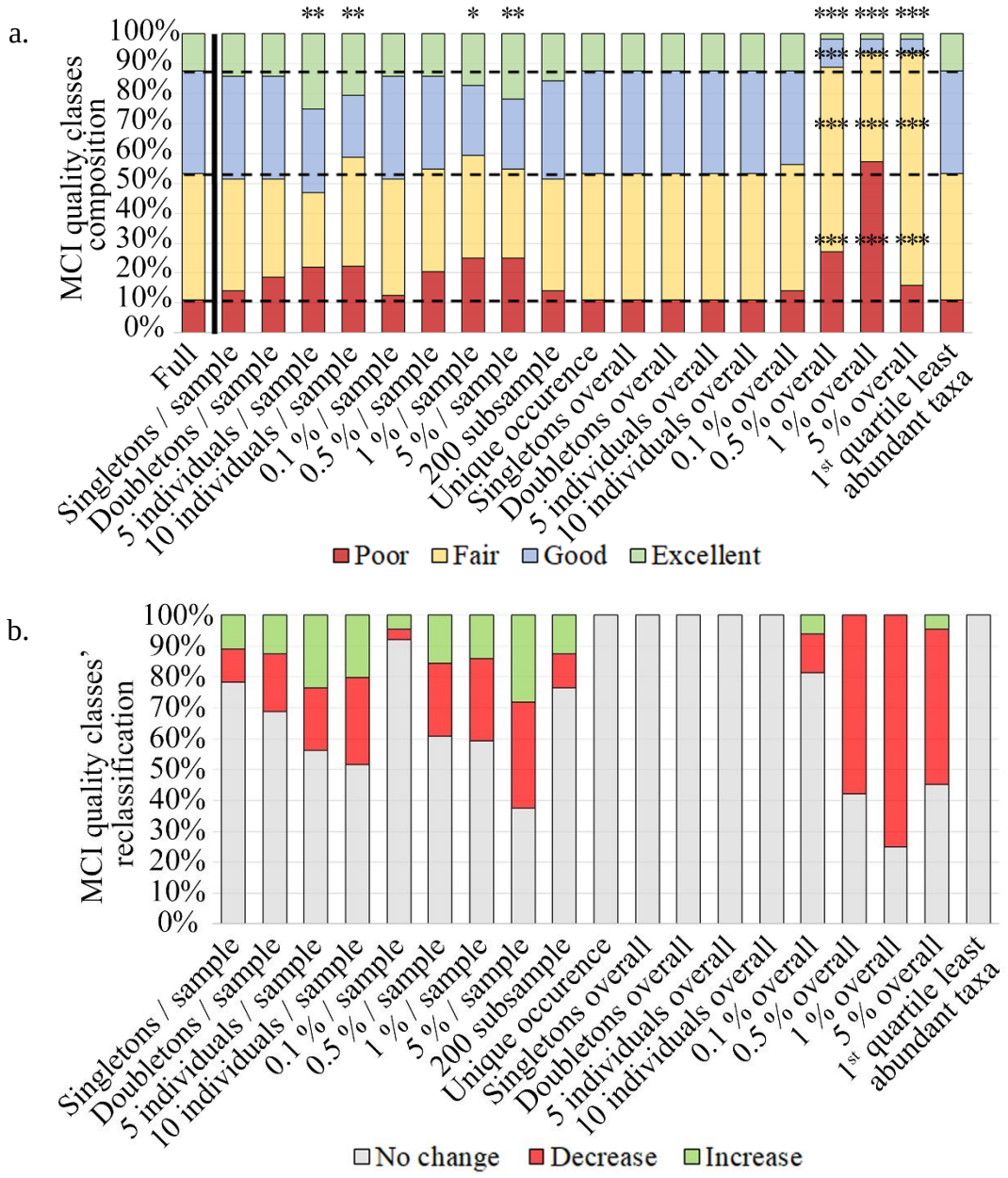

Figure 2.2: a) MCI stream health quality class composition for the full dataset and after the exclusion of rare taxa. Samples were collected in 64 streams and rivers across New Zealand during the austral summer and autumn of 2005, after exclusion of rare taxa based on the criteria listed on the x-axis. Dashed lines separate the quality classes of the full dataset. Significant X^2 differences between MCI quality classification frequencies of the full dataset and those of the datasets without rare taxa are indicated by "*" above the bars. Significant GLM differences between the mean MCI of the full dataset and those without rare taxa for each quality class of the former are indicated by "*" inside the bars. Significance levels: * < 0.05, ** < 0.01, *** <0.001; (b) MCI stream health quality class reclassification percentages.

Site-specific rarity criteria tended to exclude taxa with higher MCI scores than the common taxa in excellent and poor quality sites, albeit they didn't always differ statistically (Table 2.4a – Appendix A: Table S2.2). Mean MCI of common taxa across datasets in excellent quality sites ranged from 6.5 to 7.1, while that of rare taxa from 7 to 7.5. In poor quality sites, mean MCI of common taxa ranged from 3.4 to 4, while that of rare taxa from 4.1 to 5. Relationships between the MCI scores of common and rare taxa were more mixed, without significant differences in the good and fair quality sites. Study-wide rarity criteria also resulted in mixed relationships between mean MCI scores of common and rare taxa, with significant differences found when relative abundance criteria were applied in sites of excellent, good and fair quality. Mean MCI scores of the excellent, good and fair quality groups of sites differed significantly from the full dataset when taxa with relative abundance ≤ 0.5, 1 and 5 % of the total abundance study-wide were excluded (Fig. 2.2a – Appendix A: Table S2.1a)

Correlation between the full dataset's MCI values and those calculated after excluding the rare taxa indicated that the biggest decrease came from excluding taxa with abundance ≤ 5 % of the total, site-specifically ($r_p = 0.6$) or study-wide ($r_p = 0.68$) (Table 2.5). But the biggest qualitative change was caused by excluding taxa with study-wide relative abundance ≤ 0.5 %, 1 % and 5 % (Fig. 2.3), which led to consistent underestimation of the MCI, mostly in higher quality streams. Mean MCI of excellent quality streams dropped from 141 to 108-115 when we applied these criteria. Mean MCI of good quality streams dropped from 120 to 91-103. Mean MCI of fair quality streams dropped from 101 to 84-93. Mean MCI of poor quality streams (79) remained between 72 and 80 (Appendix A: Table S2.1a).

In the original data the QMCI indicated 20 sites were of excellent quality, 12 good, 15 fair and 17 of poor quality. None of the rare taxa exclusions lead to major

reclassifications of the sites (Table 2.3). The biggest effect was caused by the exclusion of taxa with ≤ 0.5, 1 and 5 % of the total abundance study-wide, which downgraded 6, 7 and 7 sites and upgraded 2, 2, and 4, respectively.

Taxa excluded from excellent quality sites based on site-specific criteria, tended to have lower average MCI scores (ranging from 5.7 to 6.1 across datasets) than the retained common taxa (6.1 to 6.8) (Table 2.4b – Appendix A: Table S2.2). In poor quality sites, average MCI score of rare taxa (ranged from 5 to 5.6) was significantly higher than that of common taxa (3.7 to 4.7) in all datasets. Differences in good and fair quality sites, albeit not significant, followed the same trend as the poor quality sites, with rare taxa having higher average MCI scores than common ones. Exclusion of rare taxa based on study-wide criteria had mixed effects on the relationships between the average MCI scores of common and rare taxa; only the 5% study-wide relative abundance limit resulted in statistically higher average MCI scores for common taxa in all four quality classes. Mean QMCI did not differ between the full dataset and the reduced datasets for any quality class.

Correlation between QMCI values of the full dataset and after exclusion of rare taxa was always high; the lowest correlation ($r_p = 0.94$) was found when taxa with ≤ 5 % of the total abundance study-wide were excluded (Table 2.5), resulting in the maximum change for excellent quality streams, with a lower average QMCI score (6.9) than the full dataset (7.2) (Appendix A: Table S2.1b).

Table 2.4: Mean MCI scores of the taxa comprising the common and rare components of macroinvertebrate communities in excellent, good, fair and poor quality sites, as indicated by (a) the MCI and (b) the QMCI. Common and rare components were defined based on multiple rarity definitions, presented in Table 2.1. Samples were collected from 64 streams and rivers across New Zealand during the austral Summer and Autumn 2005. Datasets with no test results had rare components with not enough taxa to perform the analyses

a. **MCI**	Excellent			Good			Fair			Poor		
	Com	Rare	$t_{(df)}$	Com	Rare	$t_{(df)}$	Com	Rare	$t_{(df)}$	Com	Rare	$t_{(df)}$
singletons / sample	6.9	7.3	$-0.62_{(6)}$	6.0	5.9	$0.38_{(20)}$	5.0	5.2	$-0.52_{(25)}$	3.8	4.9	$-2.09_{(5)}$
doubletons / sample	6.8	7.5	$-1.21_{(7)}$	6.0	5.9	$0.16_{(20)}$	5.0	5.1	$-0.21_{(26)}$	3.6	4.5	$-1.95_{(6)}$
5 individuals / sample	6.9	7.3	$-1.21_{(7)}$	6.1	5.9	$0.69_{(21)}$	5.2	5.1	$0.26_{(26)}$	**3.4**	**4.6**	**$-2.92_{(6)}$** *
10 individuals / sample	6.6	7.3	$-1.90_{(6)}$	5.9	6.2	$-0.99_{(21)}$	5.2	5.0	$0.89_{(26)}$	**3.4**	**4.5**	**$-2.54_{(6)}$** *
0.1 % / sample	7.0	7.5	$-0.99_{(2)}$	6.0	5.9	$0.28_{(13)}$	5.0	5.4	$-1.82_{(17)}$	3.9	5.0	$-1.17_{(1)}$
0.5 % / sample	**6.8**	**7.6**	**$-2.58_{(5)}$***	6.0	5.8	$0.53_{(20)}$	4.9	5.3	$-1.64_{(23)}$	**3.5**	**4.9**	**$-4.31_{(4)}$** *
1 % / sample	6.9	7.3	$-1.18_{(5)}$	5.8	6.1	$-1.17_{(21)}$	4.9	5.1	$-0.89_{(25)}$	3.4	4.5	$-2.08_{(4)}$
5% / sample	6.5	7.4	$-1.79_{(6)}$	5.6	6.1	$-1.42_{(21)}$	5.2	5.1	$0.15_{(26)}$	3.4	4.1	$-1.69_{(6)}$
200 subsample	7.1	7.0	$0.07_{(5)}$	6.0	6.0	$-0.55_{(20)}$	5.1	5.0	$0.48_{(22)}$	4.0	4.1	$1.13_{(4)}$
unique occurrence	5.8	6.0	-	5.8	6.5	$-0.49_{(1)}$	5.6	5.4	$0.75_{(5)}$	5.3	5.0	$0.89_{(2)}$
singletons overall	5.3	-	-	5.4	-	-	5.6	5.5	$-0.27_{(4)}$	6.1	-	-
doubletons overall	5.4	5.4	$-0.36_{(1)}$	5.1	6.0	-	5.1	5.7	$-1.11_{(5)}$	5.3	5.1	-
5 individuals overall	5.4	4.8	$0.73_{(3)}$	5.3	4.6	$2.13_{(7)}$	5.4	6.0	$-0.99_{(8)}$	5.5	6.6	$-1.36_{(2)}$
10 individuals overall	5.2	6.3	$-1.60_{(4)}$	5.2	5.6	$-0.49_{(8)}$	5.3	5.5	$-0.38_{(14)}$	5.4	5.5	$-0.38_{(2)}$
0.1% overall	**5.5**	**4.4**	**$2.95_{(7)}$***	5.5	5.2	$0.84_{(20)}$	5.4	5.9	$-1.72_{(22)}$	5.4	5.8	$-0.61_{(5)}$
0.5% overall	5.8	5.6	$0.61_{(6)}$	**5.6**	**6.0**	**$-4.20_{(21)}$*** **	5.6	5.6	$-0.10_{(26)}$	5.5	5.8	$-0.83_{(6)}$
1% overall	5.3	5.4	$-0.25_{(6)}$	**5.5**	**5.2**	**$2.11_{(21)}$***	5.6	5.4	$1.09_{(26)}$	5.7	5.6	$0.38_{(6)}$
5% overall	5.3	4.9	$1.26_{(6)}$	**5.4**	**4.8**	**$5.69_{(21)}$*** **	**5.5**	**4.8**	**$3.99_{(26)}$*** **	5.6	5.3	$1.10_{(6)}$
25% least abundant taxa	6.0	6.3	$-0.45_{(2)}$	6.0	5.5	$0.54_{(5)}$	6.1	5.5	$1.87_{(8)}$	6.4	5.6	$0.80_{(2)}$

b. **QMCI**	Excellent			Good			Fair			Poor		
	Com	Rare	$t_{(df)}$	Com	Rare	$t_{(df)}$	Com	Rare	$t_{(df)}$	Com	Rare	$t_{(df)}$
singletons / sample	6.2	6.1	$0.12_{(18)}$	5.6	5.6	$-0.19_{(9)}$	5.4	5.3	$0.39_{(14)}$	**4.6**	**5.4**	**$-3.18_{(15)}$** **
doubletons / sample	6.3	6.0	$0.97_{(18)}$	5.5	5.9	$-0.81_{(11)}$	5.5	5.4	$0.35_{(14)}$	**4.4**	**5.2**	**$-3.33_{(16)}$** **
5 individuals / sample	**6.6**	**5.9**	**$2.38_{(19)}$***	5.5	5.9	$-0.73_{(11)}$	5.4	5.4	$-0.03_{(14)}$	**4.3**	**5.1**	**$-3.79_{(16)}$** **
10 individuals / sample	**6.6**	**6.0**	**$2.19_{(18)}$***	5.3	5.9	$-1.31_{(11)}$	5.3	5.5	$-0.64_{(14)}$	**4.2**	**5.1**	**$-4.57_{(16)}$*** **
0.1 % / sample	6.2	5.7	$0.55_{(10)}$	5.5	5.9	$-1.76_{(8)}$	5.5	5.7	$-0.48_{(8)}$	**4.7**	**5.6**	**$-2.38_{(7)}$** *
0.5 % / sample	6.3	5.9	$1.74_{(14)}$	5.5	5.6	$-0.13_{(10)}$	5.3	5.7	$-1.43_{(14)}$	**4.2**	**5.6**	**$-5.22_{(14)}$*** **
1 % / sample	6.3	5.9	$1.16_{(17)}$	5.4	5.9	$-1.76_{(10)}$	5.2	5.5	$-0.80_{(14)}$	**4.1**	**5.4**	**$-6.35_{(14)}$*** **
5% / sample	**6.8**	**6.0**	**$2.12_{(18)}$***	5.3	6.0	$-1.57_{(11)}$	5.2	5.5	$-1.13_{(14)}$	**3.7**	**5.0**	**$-4.87_{(16)}$*** **
200 subsample	6.1	6.1	$-1.57_{(14)}$	5.6	5.7	$0.10_{(9)}$	5.5	5.4	$1.61_{(14)}$	4.8	4.9	$0.46_{(14)}$
unique occurrence	5.8	6.2	$-0.75_{(3)}$	**5.7**	**5.1**	**$16.45_{(1)}$***	5.8	5.4	$0.21_{(1)}$	5.4	5.1	$0.13_{(3)}$
singletons overall	5.5	6.1	$-4.25_{(1)}$	5.6	-	-	5.4	5.0	$1.18_{(1)}$	5.8	5.4	-
doubletons overall	5.1	5.4	$-0.72_{(3)}$	5.4	6.0	-	5.1	5.3	$0.09_{(2)}$	5.1	6.3	$-0.78_{(1)}$
5 individuals overall	5.4	5.1	$0.98_{(9)}$	5.3	4.4	$2.27_{(4)}$	5.4	6.8	$-2.04_{(3)}$	5.5	5.9	$-0.54_{(4)}$
10 individuals overall	5.2	6.1	$-1.83_{(10)}$	5.3	5.4	$-0.08_{(6)}$	**5.3**	**4.7**	**$3.08_{(6)}$** *	5.3	6.1	$-1.85_{(6)}$
0.1% overall	5.4	5.0	$1.31_{(16)}$	5.5	5.4	$0.13_{(10)}$	5.5	5.5	$-0.07_{(13)}$	5.4	5.8	$-1.05_{(15)}$
0.5% overall	5.6	5.7	$-0.41_{(18)}$	5.7	5.6	$0.42_{(11)}$	**5.5**	**5.9**	**$-3.66_{(14)}$** **	5.6	5.9	$-1.58_{(16)}$
1% overall	5.4	5.4	$0.01_{(18)}$	5.6	5.4	$1.17_{(11)}$	5.5	5.3	$1.57_{(14)}$	5.6	5.3	$1.77_{(16)}$
5% overall	**5.4**	**4.8**	**$2.76_{(18)}$***	**5.5**	**4.4**	**$4.25_{(11)}$*** **	**5.5**	**5.1**	**$2.77_{(14)}$** *	**5.5**	**5.1**	**$3.27_{(16)}$** **
25% least abundant taxa	6.0	5.6	$0.47_{(7)}$	6.0	6.0	$0.02_{(3)}$	6.1	5.8	$0.32_{(3)}$	6.2	5.4	$1.91_{(4)}$

t = t-test statistic; df = degrees of freedom

Significance levels: * < 0.05, ** < 0.01, *** < 0.001

Table 2.5: Pearson correlations between the MCI / QMCI of the full macroinvertebrate datasets and after excluding rare taxa, from samples collected in 64 streams and rivers across New Zealand, during the austral summer and autumn of 2005. All correlations were significant (p-value < 0.001) and hence no relevant indication is given.

	~MCI		~QMCI	
	$t_{(df)}$	r_p	$t_{(df)}$	r_p
singletons / sample	$19.59_{(62)}$	0.93	$215.78_{(62)}$	1.00
doubletons / sample	$15.15_{(62)}$	0.89	$203.13_{(62)}$	1.00
5 individuals / sample	$9.92_{(62)}$	0.78	$87.77_{(62)}$	1.00
10 individuals / sample	$7.72_{(61)}$	0.70	$72.29_{(61)}$	0.99
0.1 % / sample	$28.61_{(62)}$	0.96	$3665.84_{(62)}$	1.00
0.5 % / sample	$14.61_{(62)}$	0.88	$629.11_{(62)}$	1.00
1 % / sample	$11.64_{(62)}$	0.83	$327.35_{(62)}$	1.00
5% / sample	$5.96_{(62)}$	0.60	$80.17_{(62)}$	1.00
200 subsample	$17.38_{(62)}$	0.91	$24.51_{(62)}$	0.95
unique occurrence	$113.01_{(62)}$	1.00	$620.25_{(62)}$	1.00
singletons overall	$218.68_{(62)}$	1.00	$9408.20_{(62)}$	1.00
doubletons overall	$107.21_{(62)}$	1.00	$779.52_{(62)}$	1.00
5 individuals overall	$66.27_{(62)}$	0.99	$478.86_{(62)}$	1.00
10 individuals overall	$63.91_{(62)}$	0.99	$448.92_{(62)}$	1.00
0.1% overall	$29.75_{(62)}$	0.97	$118.13_{(62)}$	1.00
0.5% overall	$14.34_{(61)}$	0.88	$31.88_{(61)}$	0.97
1% overall	$8.81_{(61)}$	0.75	$26.16_{(61)}$	0.96
5% overall	$7.32_{(61)}$	0.68	$21.58_{(61)}$	0.94
25% least abundant taxa	$77.27_{(62)}$	0.99	$479.66_{(62)}$	1.00

t = test statistic; df = degrees of freedom; r_p = Pearson correlation coefficient

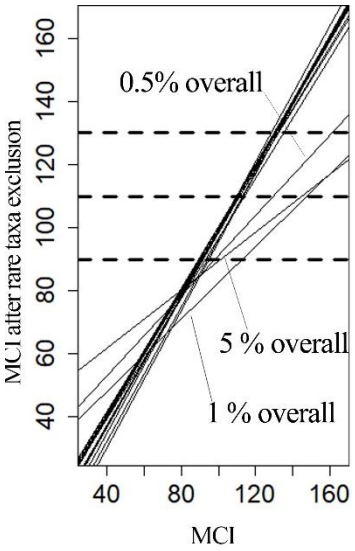

Figure 2.3: Correlation trendlines between the MCI calculated from the full dataset of 64 streams and rivers across New Zealand and the MCI calculated after the exclusion of rare taxa based on a series of criteria (Table 2.1). Samples were collected in the austral summer and autumn of 2005.

PERMANOVA comparison of biological data characterized into the four quality classes based on the MCI and QMCI from the original dataset indicated only small effects from deleting rare taxa (Table 2.6). Site-specific rarity criteria reduced the pseudo-F ratio and the adjusted R^2 for MCI-based quality classes, mostly reducing the distinctiveness between the excellent and good quality class groups when the wider absolute and relative abundance criteria were applied. Study-wide relative abundance rarity criteria on the other hand slightly increased the pseudo-F ratio and adjusted R^2. The distinctiveness between the QMCI-based quality classes also slightly increased after the rarity criteria were applied, mostly the wider relative abundance ones, which strengthened distinctiveness between good and fair quality class groups. The 2^{nd}-stage analysis indicated that most of the matrices were strongly correlated with the original data (r_s ranged between 0.84 and 1) (Fig. 2.4). The most distinct communities were the 200-individual subsamples ($r_s = 0.77$) and those excluding taxa with ≤ 5% of the site-specific total abundance ($r_s = 0.67$).

MCI declined as both NOx and DRP increased (Fig. 2.5). The effect of NOx was significant for all rare taxa-free subsets and in most cases revealed the same rate of change for MCI along the nutrient gradient (Table 2.7). However, when taxa were excluded based on their study-wide relative abundances, the MCI changed more gradually as a result of downgrading high quality sites. In contrast, site-specific exclusion of taxa increased the slope of the regression, making the MCI more responsive to nutrient concentration changes, with the most abrupt changes of the MCI along the NOx gradient seen when taxa with ≤ 5 individuals or 5 % relative abundance were excluded. The response to DRP was similar; exclusion of taxa based on site-specific criteria increased the slope of the regression and exclusion based on overall criteria reduced the slope.

The QMCI was also negatively linked with increasing levels of NOx (Table 2.7 – Fig. 2.5). Only the datasets excluding taxa with ≤ 0.5, 1 and 5 % of the total abundance study-wide did not have a significant relationship. The rest of the datasets had similar patterns to the full dataset. Albeit also showing a general negative relationship with the DRP concentration, neither the QMCI of the full dataset, nor of any of the rare taxa- taxa-excluding datasets indicated any significant regressions.

The relationship between community structure and nutrients differed between datasets (Table 2.8). Both nutrients were correlated with the second axis of the NMDS for the full dataset. NOx correlated significantly with all datasets excluding rare taxa, except for the 200-individuals subsample and when rare taxa were defined as having site-specific abundance > 2 individuals or > 0.1 % of the total abundance. DRP had fewer and weaker relationships with the ordinations than NOx did. The lower study-wide abundance and relative abundance limits (≤ 5 individuals or ≤ 0.1 %) and the first quartile limit revealed the relationship indicated by the full dataset.

Table 2.6: Permutational Analysis of Variance and pairwise significance values among stream health quality classes indicated by the MCI and the QMCI of the full macroinvertebrate datasets and after excluding rare taxa, from samples collected in 64 streams and rivers across New Zealand, during the austral summer and autumn of 2005.

	MCI class					QMCI class				
Biotic matrix	$F_{(df)}$	adj.R2	Excellent - Good	Good - Fair	Fair - Poor	$F_{(df)}$	adj.R2	Excellent - Good	Good - Fair	Fair - Poor
Full dataset	$8.72_{(1,62)}$	0.12	**0.01**	**0.01**	**0.03**	$6.50_{(1,62)}$	0.09	0.16	0.10	**0.01**
singletons / sample	$8.12_{(1,62)}$	0.12	**0.04**	**0.01**	**0.04**	$7.31_{(1,62)}$	0.11	0.13	0.13	**0.01**
doubletons / sample	$7.51_{(1,62)}$	0.11	**0.03**	**0.01**	**0.04**	$7.65_{(1,62)}$	0.11	0.13	0.13	**0.00**
5 individuals / sample	$6.51_{(1,62)}$	0.10	0.11	**0.01**	**0.04**	$8.10_{(1,62)}$	0.12	0.13	**0.02**	**0.00**
10 individuals / sample	$6.75_{(1,61)}$	0.10	0.18	**0.01**	**0.04**	$8.56_{(1,61)}$	0.12	0.06	**0.01**	**0.00**
0.1 % / sample	$8.53_{(1,62)}$	0.12	**0.03**	**0.01**	**0.03**	$6.84_{(1,62)}$	0.10	0.13	0.11	**0.00**
0.5 % / sample	$7.70_{(1,62)}$	0.11	0.05	**0.01**	**0.02**	$8.60_{(1,62)}$	0.12	0.08	**0.03**	**0.00**
1 % / sample	$7.32_{(1,62)}$	0.11	**0.03**	**0.01**	**0.03**	$8.84_{(1,62)}$	0.12	0.07	**0.01**	**0.00**
5% / sample	$5.28_{(1,61)}$	0.08	0.46	**0.01**	**0.05**	$9.86_{(1,61)}$	0.14	0.26	0.26	**0.00**
200 subsample	$8.65_{(1,62)}$	0.12	**0.03**	**0.01**	**0.01**	$7.61_{(1,62)}$	0.11	0.12	0.41	**0.00**
unique occurrence	$8.82_{(1,62)}$	0.12	**0.03**	**0.01**	**0.03**	$6.57_{(1,62)}$	0.10	0.17	0.10	**0.01**
singletons overall	$8.73_{(1,62)}$	0.12	**0.02**	**0.01**	**0.03**	$6.51_{(1,62)}$	0.10	0.18	0.11	**0.00**
doubletons overall	$8.76_{(1,62)}$	0.12	**0.04**	**0.01**	**0.03**	$6.54_{(1,62)}$	0.10	0.18	0.08	**0.00**
5 individuals overall	$8.88_{(1,62)}$	0.13	**0.04**	**0.01**	**0.03**	$6.61_{(1,62)}$	0.10	0.18	0.11	**0.01**
10 individuals overall	$8.95_{(1,62)}$	0.13	**0.04**	**0.00**	**0.04**	$6.67_{(1,62)}$	0.10	0.18	0.05	**0.00**
0.1% overall	$10.19_{(1,62)}$	0.14	**0.02**	**0.01**	**0.04**	$7.63_{(1,62)}$	0.11	0.13	0.09	**0.00**
0.5% overall	$9.74_{(1,61)}$	0.14	**0.06**	**0.01**	**0.02**	$8.50_{(1,61)}$	0.12	0.14	0.07	**0.00**
1% overall	$10.46_{(1,61)}$	0.15	**0.05**	**0.02**	**0.02**	$10.16_{(1,61)}$	0.14	0.09	0.06	**0.00**
5% overall	$10.41_{(1,61)}$	0.15	**0.04**	**0.03**	**0.04**	$10.32_{(1,61)}$	0.14	0.08	**0.04**	**0.01**
25% least abundant taxa	$8.88_{(1,62)}$	0.13	**0.03**	**0.01**	**0.03**	$6.61_{(1,62)}$	0.10	0.19	0.10	**0.00**

Significance level: < 0.05

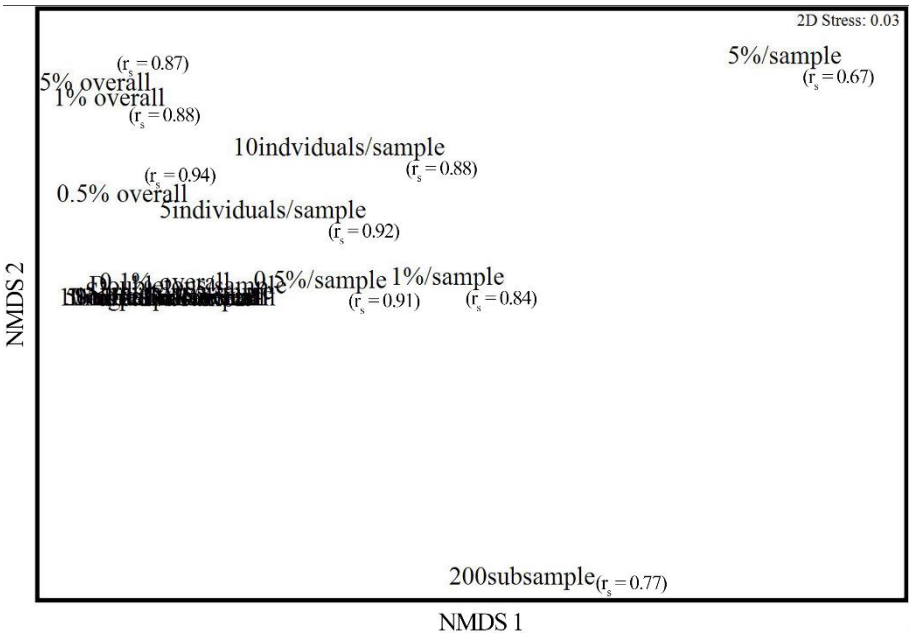

Figure 2.4: 2nd-stage NMDS of the full dataset and the datasets after the exclusion of rare taxa based on a series of criteria (Table 2.1), from samples collected in 64 streams and rivers across New Zealand, during the austral summer and autumn of 2005. r_s = Spearman's rank correlation statistic.

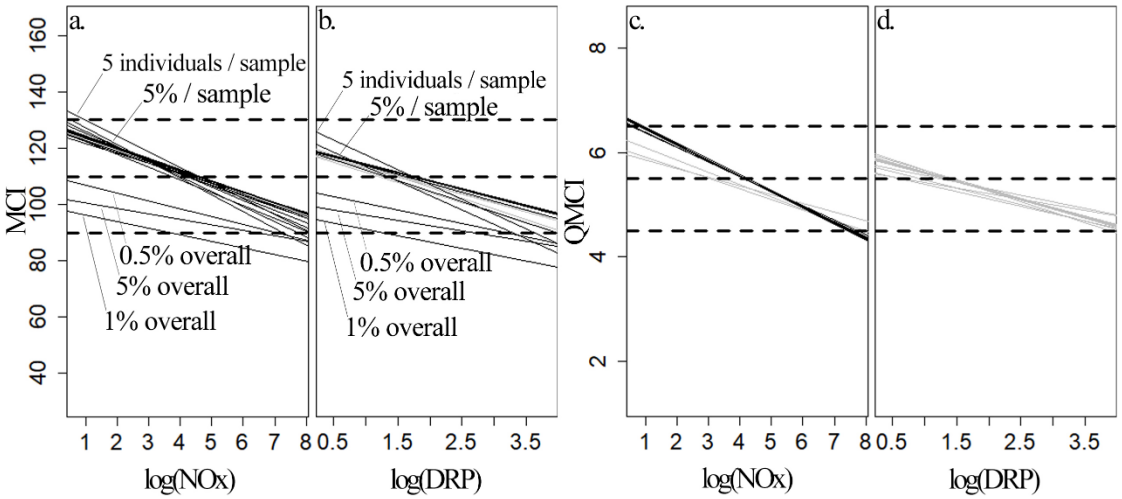

Figure 2.5: Linear regression trendlines between stream health quality indices, MCI and QMCI, and log-transformed annual medians of NOx and DRP concentration. The samples were collected from 64 streams and rivers across New Zealand. Macroinvertebrates were sampled during the austral summer and autumn of 2005. Index values were calculated for the full datasets and after excluding rare taxa based on the criteria listed in Table 2.1. Nutrient measurements were recorded monthly during 2004. Black trendlines indicate significant regressions as opposed to grey trendlines for non-significant ones (significance level < 0.05).

Table 2.7: Linear regressions between the 2004 annual median NOx and DRP concentrations and the 2005 MCI and QMCI of the full macroinvertebrate datasets and after excluding rare taxa, from samples collected in 64 streams and rivers across New Zealand.

	MCI						QMCI					
	NOx			DRP			NOx			DRP		
	Slope	adj.R2	F-stat$_{(df)}$	Slope	adj.R2	F-stat	Slope	adj.R2	F-stat	Slope	adj.R2	F-stat
Full dataset	**-3.92**	**0.11**	**8.94$_{(1,62)}$****	**-6.09**	**0.05**	**4.62$_{(1,62)}$***	**-0.30**	**0.08**	**6.40***	-0.04	0.02	2.13
singletons / sample	**-3.84**	**0.08**	**6.76$_{(1,62)}$***	-5.36	0.03	2.84$_{(1,62)}$	**-0.30**	**0.08**	**6.45***	-0.04	0.02	2.08
doubletons / sample	**-4.39**	**0.10**	**8.35$_{(1,62)}$****	-6.29	0.04	3.66$_{(1,62)}$	**-0.30**	**0.08**	**6.28***	-0.04	0.01	1.96
5 individuals / sample	**-5.59**	**0.12**	**9.68$_{(1,62)}$****	**-10.6**	**0.10**	**7.66$_{(1,62)}$****	**-0.30**	**0.07**	**6.07***	-0.04	0.02	2.01
10 individuals / sample	**-4.78**	**0.09**	**6.94$_{(1,61)}$***	-7.73	0.04	3.92$_{(1,62)}$	**-0.28**	**0.06**	**4.93***	-0.03	0.00	1.21
0.1 % / sample	**-4.14**	**0.12**	**9.36$_{(1,62)}$****	**-6.34**	**0.06**	**4.69$_{(1,62)}$***	**-0.30**	**0.08**	**6.40***	-0.04	0.02	2.13
0.5 % / sample	**-5.32**	**0.14**	**11.6$_{(1,62)}$****	**-7.52**	**0.06**	**4.82$_{(1,62)}$***	**-0.30**	**0.08**	**6.42***	-0.04	0.02	2.10
1 % / sample	**-4.55**	**0.08**	**6.76$_{(1,62)}$***	-7.21	0.04	3.72$_{(1,62)}$	**-0.30**	**0.08**	**6.15***	-0.04	0.02	1.99
5% / sample	**-6.00**	**0.10**	**8.27$_{(1,62)}$****	**-10.3**	**0.06**	**5.34$_{(1,62)}$***	**-0.30**	**0.07**	**5.74***	-0.04	0.01	1.69
200 subsample	**-3.89**	**0.09**	**7.44$_{(1,62)}$****	-5.94	0.04	3.76$_{(1,62)}$	**-0.30**	**0.08**	**6.45***	-0.04	0.02	1.98
unique occurrence	**-3.84**	**0.11**	**8.71$_{(1,62)}$****	**-5.70**	**0.05**	**4.10$_{(1,62)}$***	**-0.30**	**0.08**	**6.32***	-0.04	0.02	2.09
singletons overall	**-3.90**	**0.11**	**8.75$_{(1,62)}$****	**-6.02**	**0.05**	**4.48$_{(1,62)}$***	**-0.30**	**0.08**	**6.39***	-0.04	0.02	2.13
doubletons overall	**-3.90**	**0.11**	**8.77$_{(1,62)}$****	**-6.04**	**0.05**	**4.52$_{(1,62)}$***	**-0.30**	**0.08**	**6.42***	-0.04	0.02	2.14
5 individuals overall	**-3.85**	**0.11**	**8.77$_{(1,62)}$****	**-5.78**	**0.05**	**4.23$_{(1,62)}$***	**-0.30**	**0.08**	**6.34***	-0.04	0.02	2.08
10 individuals overall	**-3.89**	**0.11**	**8.62$_{(1,62)}$****	**-5.93**	**0.05**	**4.29$_{(1,62)}$***	**-0.30**	**0.08**	**6.30***	-0.04	0.02	2.07
0.1% overall	**-3.51**	**0.07**	**5.94$_{(1,62)}$***	-5.52	0.03	3.22$_{(1,62)}$	**-0.29**	**0.07**	**5.60***	-0.04	0.01	1.95
0.5% overall	**-2.76**	**0.11**	**8.99$_{(1,61)}$****	**-4.77**	**0.07**	**5.90$_{(1,62)}$***	-0.24	0.04	3.81	-0.04	0.01	1.85
1% overall	**-2.32**	**0.07**	**5.33$_{(1,61)}$***	**-4.48**	**0.05**	**4.54$_{(1,62)}$***	-0.20	0.03	2.78	-0.03	0.01	1.41
5% overall	**-1.93**	**0.06**	**4.83$_{(1,61)}$***	**-3.73**	**0.05**	**4.12$_{(1,62)}$***	-0.17	0.02	1.99	-0.03	0.00	1.08
25% least abundant taxa	**-3.96**	**0.11**	**9.06$_{(1,62)}$****	**-5.92**	**0.05**	**4.31$_{(1,62)}$***	**-0.30**	**0.08**	**6.34***	-0.04	0.02	2.08

Significance levels: * < 0.05, ** < 0.01, *** < 0.001

Table 2.8: Linear regression between the 2004 annual median NOx and DRP concentrations and the two axes of the NMDS ordinations of macroinvertebrate communities collected in 64 streams and rivers across New Zealand in 2005, and after the exclusion of rare taxa.

	NOx				DRP			
	NMDS1		NMDS2		NMDS1		NMDS2	
	adj.R2	F-stat$_{(df)}$	adj.R2	F-stat$_{(df)}$	adj.R2	F-stat$_{(df)}$	adj.R2	F-stat$_{(df)}$
Full dataset	-0.01	0.45$_{(1,62)}$	**0.06**	**5.13$_{(1,62)}$***	-0.02	0.02$_{(1,62)}$	**0.05**	**4.12$_{(1,62)}$***
singletons / sample	-0.02	0.05$_{(1,62)}$	**0.07**	**6.03$_{(1,62)}$***	-0.01	0.33$_{(1,62)}$	0.04	3.53$_{(1,62)}$
doubletons / sample	-0.01	0.39$_{(1,62)}$	**0.07**	**5.58$_{(1,62)}$***	-0.01	0.14$_{(1,62)}$	**0.05**	**4.42$_{(1,62)}$***
5 individuals / sample	0.00	1.06$_{(1,62)}$	0.04	3.45$_{(1,62)}$	-0.02	0.05$_{(1,62)}$	0.04	3.68$_{(1,62)}$
10 individuals / sample	0.01	1.72$_{(1,61)}$	0.01	1.52$_{(1,61)}$	-0.01	0.28$_{(1,61)}$	0.03	2.90$_{(1,61)}$
0.1 % / sample	-0.01	0.61$_{(1,62)}$	**0.05**	**4.21$_{(1,62)}$***	-0.02	0.01$_{(1,62)}$	0.03	3.20$_{(1,62)}$
0.5 % / sample	0.02	2.45$_{(1,62)}$	0.02	2.19$_{(1,62)}$	-0.01	0.37$_{(1,62)}$	0.03	3.14$_{(1,62)}$
1 % / sample	0.01	1.61$_{(1,62)}$	0.01	1.52$_{(1,62)}$	-0.01	0.08$_{(1,62)}$	0.02	2.02$_{(1,62)}$
5% / sample	0.03	3.20$_{(1,62)}$	0.00	0.85$_{(1,62)}$	-0.01	0.22$_{(1,62)}$	-0.01	0.11$_{(1,62)}$
200 subsample	0.02	2.14$_{(1,62)}$	0.01	1.42$_{(1,62)}$	0.00	0.83$_{(1,62)}$	0.00	0.93$_{(1,62)}$
unique occurrence	-0.01	0.38$_{(1,62)}$	**0.07**	**5.45$_{(1,62)}$***	-0.02	0.05$_{(1,62)}$	0.04	3.75$_{(1,62)}$
singletons overall	-0.01	0.48$_{(1,62)}$	**0.06**	**5.15$_{(1,62)}$***	-0.02	0.02$_{(1,62)}$	**0.05**	**4.16$_{(1,62)}$***
doubletons overall	-0.01	0.46$_{(1,62)}$	**0.06**	**5.15$_{(1,62)}$***	-0.02	0.03$_{(1,62)}$	**0.05**	**4.14$_{(1,62)}$***
5 individuals overall	-0.01	0.39$_{(1,62)}$	**0.06**	**5.27$_{(1,62)}$***	-0.02	0.03$_{(1,62)}$	**0.05**	**4.09$_{(1,62)}$***
10 individuals overall	-0.01	0.40$_{(1,62)}$	**0.06**	**5.36$_{(1,62)}$***	-0.02	0.04$_{(1,62)}$	0.04	3.63$_{(1,62)}$
0.1% overall	-0.01	0.68$_{(1,62)}$	**0.06**	**4.71$_{(1,62)}$***	-0.02	0.00$_{(1,62)}$	**0.06**	**4.92$_{(1,62)}$***
0.5% overall	**0.07**	**5.70$_{(1,61)}$***	0.00	0.89$_{(1,61)}$	**0.06**	**5.31$_{(1,61)}$***	-0.02	0.03$_{(1,61)}$
1% overall	**0.07**	**5.66$_{(1,61)}$***	-0.01	0.12$_{(1,61)}$	**0.05**	**4.01$_{(1,61)}$***	-0.02	0.04$_{(1,61)}$
5% overall	**0.06**	**4.76$_{(1,61)}$***	-0.01	0.20$_{(1,61)}$	0.03	3.10$_{(1,61)}$	-0.01	0.21$_{(1,61)}$
25% least abundant taxa	-0.01	0.36$_{(1,62)}$	**0.07**	**5.43$_{(1,62)}$***	-0.02	0.05$_{(1,62)}$	**0.05**	**4.08$_{(1,62)}$***

Significance levels: * < 0.05, ** < 0.01, *** < 0.001

2.4 Discussion

Removal of rare taxa mostly resulted in assemblages that were structurally similar to the original ones, except for the broadest rarity definitions which excluded the highest numbers of taxa (Arscott et al., 2006). However, subsampling yielded assemblages with radically different structure from the full dataset.

2.4.1 The effect of rare taxa exclusion on MCI and QMCI

Exclusion of rare taxa had a big effect on the water quality classification using the MCI, but the QMCI classifications were more robust. The MCI detects changes in the taxonomic composition of an assemblage, while QMCI responds more to changes in the numerical composition; thus, the QMCI can be more sensitive to, potentially subtle, changes in community composition that affect species abundances but do not result in local extinctions (Stark & Maxted, 2007b). Exclusion of rare taxa always meant taxonomic change, whether the exclusion criteria were site-specific or study-wide, but its effect on the numbers of invertebrates was often comparatively small (Van Sickle et al., 2007). This led to greater effect on the MCI band assignment and minimal effect on the QMCI, corroborating our hypothesis.

Nijboer & Schmidt-Kloiber (2004) found exclusion of low abundance taxa increased the ecological quality classification along an organic pollution gradient in Dutch streams and were concerned this might not lead to mitigation action in degrading ecosystems. In the New Zealand context, rare taxa removal had mixed results when based on site-specific criteria (gradually more extensive along the gradients of abundance and relative abundance), but almost always resulted in reduced MCI classifications when removal was determined based on relative abundances across the whole study. The latter most likely resulted from the low number of remaining abundant taxa used to calculate

the index, ranging from 7 for the 5 % study-wide relative abundance limit to 14 for the 0.5 % limit (Guareschi et al., 2017). Misclassifications based on the QMCI were also mixed, with downgrading being more common, but were much more limited than the MCI ones.

Contrary to Cao et al. (2001) and Nijboer & Schmidt-Kloiber (2004), exclusion based on low occurrence frequency did not affect quality classification of any site for either index. Unique occurrences over large areas can stem from range-limited species, or stochastic events, such as lentic species (e.g. Dytiscidae and Culicidae), or species living in stream margins or seepages (e.g. *Hydrobiosella* and *Zelandotipula*) (Winterbourn et al., 2006). Vagrant species that comprise part of the rare component of assemblages, can also affect analyses at local scales (Gaston, 1994). Study-wide absolute abundance criteria applied over such a large area naturally excluded only a few tens of individuals. This number is also kept low by the fact that the lowest taxonomic level used in New Zealand stream biomonitoring is genus and thus many species that would otherwise be considered rare are probably masked by their more common congenerics (Boothroyd & Stark, 2000). The same criteria applied on a more local scale and/or on species level data could potentially distinguish a larger rare component. That may be why misclassifications from the application of site-specific absolute abundance criteria were so pronounced. A lack of effect on biotic indices was also observed after the exclusion of the 1st quartile of least abundant species, the universal rare taxa distinction method proposed by Gaston (1994). In our study the excluded component comprised 19 taxa, with abundances of less than five individuals each, summing up to only 49 individuals. Even though such a definition of rarity might conceal differences among communities with varying levels of evenness and rare components' richness (Magurran, 2004), its effect on the bioassessment of our highly uneven assemblages was minimal.

2.4.2 The effect of rare taxa exclusion on streams of differing quality

The exclusion of rare taxa resulted in assemblages whose structure was differentiated into quality classes mostly in a similar way to the original dataset. The structure of the MCI quality groups was clearly differentiated in most datasets. The wider site-specific rarity criteria masked the differences between MCI-excellent and good quality sites. As was evident from the excellent quality sites, sensitive taxa that were found in those high quality streams, were not always in high abundances and thus were filtered out as part of the rare component (Poos & Jackson, 2012). Based on the QMCI classifications, only the fair and poor-quality groups were differentiated in the original dataset. The emergence of assemblage structure differences between the good and fair quality groups of streams when the wider site-specific rarity criteria were applied are more difficult to explain. Potentially the stricter rarity limits excluded only vagrant taxa from the samples, not sufficing to differentiate the QMCI quality classes that were defined based on abundances. Wider rarity limits excluded slightly more sensitive rare taxa from both fair and good quality sites, potentially leaving taxa more representative of each class behind, and thus, more clearly differentiated assemblages. However, it seems unlikely that these sensitive taxa would mask these differences, to that they would not be observed in the full datasets. While the discovery of clear differences where they would be expected to be found can be attractive, the exclusion of rare taxa for the mere discovery of statistically strong patterns would lack ecological sense (Fore et al., 1996).

Misclassifications among the poor quality sites based on either index were rare. However, these could be quantified only when the quality class of a site was improved. Sites that were characterised by lower MCI or QMCI values were still classified as poor, and as the average MCI score was lower for common taxa than site-specific rare ones in these sites, lower MCI scores post-exclusion should be expected. Despite some very low

MCI values (site WA9 in the lower reaches of the Manawatu River had MCI = 30 when taxa with site-specific relative abundance up to 1 and 5 % were excluded from the dataset), the average MCI of the poor quality group did not differ significantly between the full community and the different datasets. Sensitive taxa were largely absent from the highly polluted sites (Nijboer & Verdonschot, 2004). Even the rare component, thus, comprised fairly tolerant and/or vagrant taxa, and consequently, the MCI was not majorly affected by the exclusion of the rare taxa (Cao et al., 1998).

On the other hand, there was significant change observed with rare taxa exclusion in the MCI of the excellent, good and fair quality sites for the 0.5, 1 and 5 % study-wide relative abundance exclusion limits, also corroborating our hypothesis that higher quality streams' assessment would be affected more than lower quality ones. The average post-exclusion MCI values always indicated lower quality streams, resulting from the exclusion of the majority of sensitive taxa, which were still rare even in excellent quality sites, as indicated by the average MCI score of taxa that were excluded with site-specific criteria (Cao et al., 1998). The heavier effect of rare taxa exclusion on high quality streams was also indicated by the good quality MCI classification of most of the originally excellent quality sites after the exclusion of taxa with ≤ 0.5 % of the total abundance study-wide, as opposed to the mixture of good and fair quality sites after the exclusion of taxa with ≤ 1 and 5 % of the total abundance study-wide. The 0.5 % limit retained only 14 very abundant taxa (among which the highly sensitive caddisfly genera *Olinga* and *Helicopsyche* – 99 % of the latter's individuals were found in a single site) and hence the average quality remained Good. The 1 and 5 % limits excluded these two genera, retaining only the relatively sensitive mayfly genus *Deleatidium* (by far the most abundant taxon in the dataset) along with moderately and very tolerant taxa (Poos & Jackson, 2012). By underestimating the sampled streams' class that was based on all taxa,

the three study-wide relative abundance criteria also interfere with the planning stages of management and restoration actions and future monitoring in two ways; funds might be directed towards sites that are of excellent quality but appear to be degraded, and more importantly, initial changes that can indicate degradation might go unnoticed until the quality of the streams is further degraded, beyond the original, false estimation (Cao & Williams, 1999; Clarke & Murphy, 2006).

2.4.3 The effect of rare taxa exclusion on assemblage-nutrient relationships

The effect of rare taxa exclusion on the relationship between the indices and the nutrients, depended on both the nutrient and the index in question, but the MCI was, in general, more affected than the QMCI, corroborating our hypothesis that the loss of rare sensitive taxa would affect the more richness based MCI than the abundance based QMCI.

NOx was more strongly related to the indices than DRP and the MCI was more strongly related to both nutrients than the QMCI. Exclusion of rare data did not mask the relationship of NOx and MCI, instead, with moderate site-specific criteria the variation explained in the model increased. These exclusion criteria excluded vagrant species that were not strongly linked with conditions in their respective samples, but also rare taxa, whose tolerance was not reflective of stream status; i.e. rare tolerant taxa from good quality streams and rare sensitive taxa from degraded streams. The study-wide relative abundance criteria reduced the explained variation. As has already been elaborated, these criteria led to very taxa-poor datasets, consisting mostly of very abundant, more or less tolerant taxa and the occasional sensitive taxa limited in only a few sites. The MCI misclassification in the excellent, good and fair quality sites, along with the non-significant difference in the poor quality sites rendered the MCI less responsive to NOx changes. This suggests that the excluded rare taxa are those sensitive ones that give a first indication of degradation (Cao & Williams, 1999; Clarke & Murphy, 2006).

The relationship between the DRP and the MCI was more affected by the exclusion of rare taxa. Several of the site-specific criteria masked that relationship, probably because it was weaker in the first place and thus more easily affected by the exclusion of rare taxa from every site. However, a similar increase in the explained variation was seen, as for NOx when the 5-individual criterion was applied. It may mean that the exclusion of species largely unrepresentative of the conditions, could facilitate interpretation of the relationship between communities and their environment (Gauch & Gauch, 1982; Marchant, 1999). Study-wide criteria mostly retained the relationship and followed similar patterns as for NOx.

The relationship between QMCI and NOx remained unaffected for most exclusion criteria, apart from those excluding the highest percentages of study-wide relative abundance. This result was probably related to the use of taxa abundances by the QMCI. The few, overly abundant and moderately tolerant taxa in these datasets could not correlate to the NOx gradient and were among themselves also very uneven, with e.g. the genus *Deleatidium* accounting for approximately 25 % of all individuals.

Both NOx and DRP were linked to the community ordination. These relationships were retained after the exclusion of rare taxa based on study-wide criteria more often than with site-specific ones, because the latter excluded more of the taxa that would place the corresponding sites along the nutrient gradient.

2.5 Conclusions

One of the presumed issues with rare taxa is their weak representativeness of the samples they are found in, both in terms of occurrence and relative abundance (Beck et al., 2013). However, in large datasets with many sampling sites and several replicate samples per site, some taxa that would be considered rare in a random sample, will not be considered

so anymore, and others that actually belong in the rare component of their communities will relate more clearly to their environment. Exclusion of rare taxa from datasets used in biomonitoring in New Zealand did not appear to be advantageous for biomonitoring tools. On the contrary, presence-absence data-based tools such as the MCI misclassified the ecological condition of many sites. The potential of rare taxa to indicate high quality conditions makes them particularly useful for accurate bioassessment (Nijboer & Schmidt-Kloiber, 2004). Rare taxa are at higher risk of local extinction because of their small populations (Purvis et al., 2000). As stream ecosystem management decisions are often site-specific, excluding rare taxa can have serious implications. Upgraded sites as a result of rare taxa exclusion can lead to a failure to detect deteriorating conditions, while downgraded excellent quality sites can direct funds and effort where they are not required (Doberstein et al., 2000; Guareschi et al., 2017). Even when the assessment outcome is not affected, their early warning potential will be lost (Cao & Williams, 1999). Consequently, there is no advantage to be gained from their exclusion and in many cases it might affect the assessment of stream ecosystem's ecological quality (Guareschi et al., 2017; Poos & Jackson, 2012). Apart from the innate value in preserving all species, future advances in taxonomic knowledge of the New Zealand macroinvertebrate fauna and potential updates of the available biomonitoring tools will require a reassessment of the effect of rare species treatment on these tools. Inclusion of rare species will be made more necessary, as species of conservation interest will then be properly recorded and incorporated in models to indicate biodiversity hotspots (Aroviita et al., 2010; Scarsbrook et al., 2000).

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Chapter 3

Exploring the effect of sampling method on inferences about rare species biodiversity in stream Trichopteran communities.

Abstract

Natural communities comprise a large number of rare species and a few common ones, but rare species are often excluded from analysis and reporting as overly variable outliers. Assessing stream biodiversity is further complicated by the fact that stream resident invertebrates are predominantly larval, and often difficult to identify to species level, necessary for finding rarer taxa. Complete biodiversity assessment of stream Trichoptera therefore usually involves additional sampling of the adult forms. We compared two benthic sampling methods (kick-net and Surber) and two traps for adult insects (UV-light and Sea-Land-Air-Malaise –SLAM– traps) for their efficiency in assessing stream Trichoptera biodiversity, also focusing on the rare components of the communities. Samples were collected from 15 streams in Tongariro National Park, New Zealand. Rare taxa were defined as those with abundance equal to or less than 10 individuals or 0.5% of the total abundance at each site. All methods collected clearly distinguishable communities. The traps did not manage to collect more taxa than the benthic methods, but the latter required many more individuals to be collected. Benthic samples were also more diverse, because of their richer rare component. Surber samples from riffle habitats collected on average ~25% more species than kick-net samples from non-riffle habitats, but the latter collected a higher portion of the γ-diversity in the study area, as they can collect more rare species from more habitats. Trap efficacy depended highly on local habitat conditions. UV-light traps collected richer and more diverse assemblages than the SLAM traps, were easier to use and required less sampling time, but also recorded species from non-stream habitats as rare, and missed species not attracted by their UV-wavelength. Traps can be a useful addition for assessment of caddisfly biodiversity and rare species but cannot substitute for benthic methods that can collect more representative samples of the stream community.

3.1 Introduction

Counterintuitive as it may seem, rare species are actually common in the natural world (Lim et al., 2012). Biological communities typically comprise a few abundant and many rare species (Gaston, 1994; Dudgeon et al., 2006). This may be even more pronounced in habitats that are little affected by human activities (Fore et al., 1996). However, despite their widespread presence in nature, and several attempts to study them, rare species remain difficult to incorporate into community ecology studies (Cao et al., 1998).

Rarity can be defined in a variety of ways (Gaston, 1994), including: species with a narrow distribution range or a narrow habitat range; those with low absolute or relative abundance; or those with low frequency of occurrence in a given number of samples (Cao et al., 1998; Faith & Norris, 1989; Rabinowitz, 1981). The causes of rarity also vary considerably; they might be related to the species' ecology, physiology or behaviour, or they might be related to certain environmental characteristics of the species' habitat. Sampling method can also determine whether a species is perceived to be rare or not (Gaston, 1994; Cao, Bark, et al., 1997). Studying rare species is thus considerably problematic, without clearly defining what is considered rare.

Including rare species in community ecology studies raises many issues. Rare species might still be undescribed (Dudgeon et al., 2006). They might be indistinguishable from other species except by taxonomic experts because of a lack of descriptive characters or effective taxonomic work (e.g. early instars of benthic macroinvertebrates (Winterbourn et al., 2006). Thus, species of conservation concern can remain completely absent from conservation plans and policies. Even when rare species can be identified and acknowledged, they might not be represented by their true relative abundance, or at all, particularly in small samples (Beck et al., 2013). A common response to their presence in communities is data removal on the grounds they provide data with a

large proportion of zeros (zero inflated data, which can potentially hamper species abundance and distribution modelling – Barry & Welsh, 2002; Welsh et al., 1996) and might obscure environmental patterns (Cao et al., 1998, 2001) while only providing redundant information (Marchant, 1999; Roden et al., 2018).

Proponents for the more widespread use of rare species in community analyses stress the innate value of every species and that they may be essential for a full understanding of monitoring to assist managing ecosystems (Mouillot et al., 2013). Furthermore, the use of the appropriate statistical analysis may enhance their value in data (Cao, Bark, et al., 1997) where the detection of subtle or early ecological change might require inclusion of rare species (Cao et al., 2001). Rare species may have distinct functional traits that are critical for functional diversity in communities and thus, be important for the maintenance of ecosystem function and services (Violle et al., 2017).

New Zealand's freshwater ecosystems are characterised by a very high degree of endemism (Death et al., 2016; Joy & Death, 2013; Boothroyd, 2000) and with upwards of 50% of their species either threatened or data deficient (Grainger et al., 2018; Joy & Death, 2013). Freshwater biomonitoring by environment agencies use macroinvertebrates extensively but usually at the genus or higher level (Joy & Death, 2013). Furthermore sampling is typically focused on riffles, where macroinvertebrates more sensitive to pollution occur (Stark et al., 2001). These microhabitats are hydromorphologically similar across streams to ensure quantitatively comparable results (Karr, 1999), but rare species in other microhabitats (e.g., pools, seepages, stream banks) will consequently be underrepresented. It is not even possible to always identify the collected larvae to species level, let alone identify rare species (Winterbourn et al., 2006; Chapman et al., 2011). Additionally, pooling species into genera might conceal their ecological differences (Heino, 2005).

The collection of adult, flying, aquatic insects is one method to aid in species level identification and has at times been suggested as a necessary part of stream surveys (Morse et al., 1980) or even a surrogate of larval assemblages (Valente-Neto et al., 2016). There is more detailed taxonomic information at the species level available for the adult insects compared to their benthic larvae (Smith, 2014), but their collection is rarely applied in benthic community ecology studies (Joy & Death, 2013).

There are many types of traps available that can be used to sample the flying stages of aquatic invertebrates: interception traps (e.g. Malaise and SLAM (Sea-Land-Air-Malaise) traps); sticky traps; emergence traps; (UV-)light traps etc. (Southwood & Henderson, 2000; Epsky et al., 2004). They can be set in the field and passively trap insects or attract phototactically and polarotactically sensitive insects (Horvath & Kriska, 2008; Price & Baker, 2016). The method used can have a significant effect on the representation of the actual community by the sample, as was found by Collier & Smith (1998) who caught different caddisfly communities with sticky and uv-light traps.

Thus, while rare species have been little studied, they may be potentially important for understanding the community ecology of benthic macroinvertebrate communities. It is challenging to know the best sampling method for collecting those rare taxa. This study aimed at assessing the effect of sampling method and life stage of freshwater caddisflies on inferences about the caddisflies' biodiversity and in comparison with the patterns describing the caddisfly communities' rare taxa components. We used four methods; two active methods to sample benthic caddisfly larvae (kick-net and Surber sampling) and two methods to sample flying adults; one active (UV-light trapping) and one passive (SLAM trapping).

3.2 Methods

3.2.1 Study sites

Sampling was conducted in and around the Tongariro National Park, in the central North Island of New Zealand. The park encompasses the central volcanic massif (Mount Ruapehu, Ngauruhoe and Tongariro) and the Tihia-Kakaramea volcanic massif to the north, which are made of andesitic rocks. The rainfall pattern differs around the Park; the north and west sides receive on average 1,800 – 3,500 mm/year, while the east and south about 1,100 mm/year because of the rain-shadow cast by the mountains of the central volcanic massif. Plant communities around the Park range from broadleaf- and mixed beech-podocarp, to exotic *Pinus radiata* plantation, native tussock and scrubland, with the rain-shadow to the east resulting in considerable sandy bare ground (Tonkin et al., 2013).

To establish the appropriate number of sampling locations for a good taxonomic inventory of the area, complete benthic macroinvertebrate communities' data collected with Surber samplers at 47 sites in the region and identified to the lowest level feasible by Tonkin et al. (2013) were evaluated. EstimateS 9.1.0 software (Colwell, 2013) was used to randomly resample those 47 sites until sampling an additional site did not add more than one taxon to the taxonomic pool of the area. The cut-off point based on that criterion was set at 16 sites. Sixteen streams were then selected from all streams in the national park for sampling in proportion to stream typology from the Freshwater Ecosystems of New Zealand database (FENZ – Leathwick et al. 2010) at a level 2 classification (this has 100 river classes for New Zealand). Selection was also based on accessibility and ensured wide spatial distribution around the national park (Fig. 3.1). In the Tongariro National Park area there were six FENZ classes (Table 3.1). The most abundant classes, C9 and G2, where characterised by relatively high flow stability and

moderate to low slope. Mature exotic forest plantations were present at three sites (Te Unuunuakapuateariki, Te Whaiau & Poutu streams), but these forest streams have similar benthic communities to native forest in New Zealand, and consequently is unlikely to affect the results (Quinn et al., 1997; 2004).

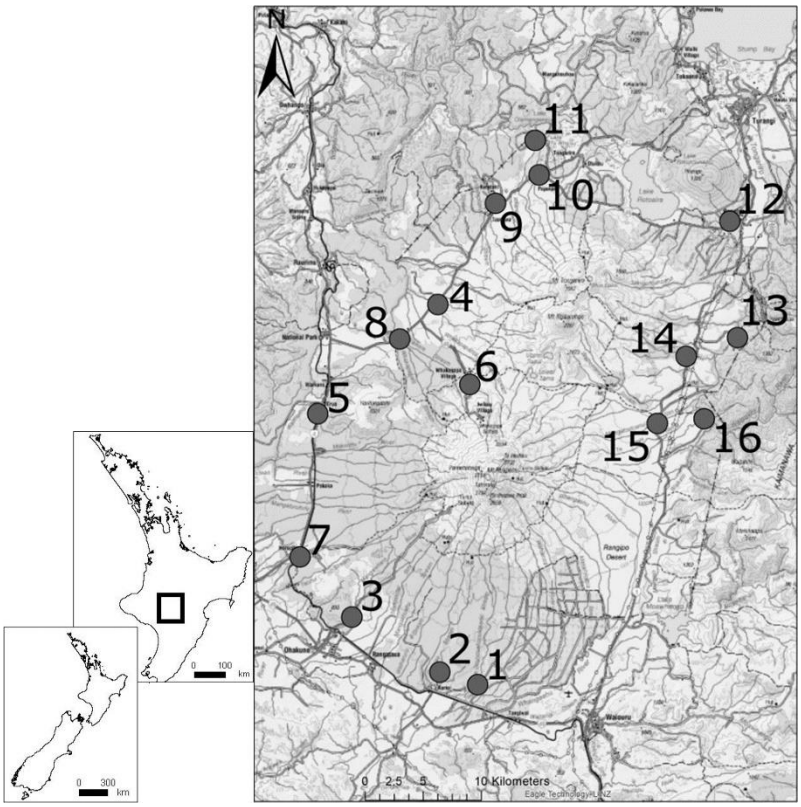

Figure 3.1: Location of 16 streams sampled in March 2017 in the Tongariro National Park, New Zealand. Numbers correspond to Table 3.1

3.2.2 Definition of rarity

Among the several criteria that have been proposed to define rare species (Rabinowitz, 1981), a combination of the absolute and relative abundance of a taxon in the sample was selected. Taxa were considered rare in a sample if their abundance was equal to or less than 10 individuals or 0.5% of the total abundance of individuals collected in that sample. These are common cut-off points set by researches to determine which species to discard from analyses (Sgarbi & Melo, 2018; Yu et al., 2017).

Table 3.1: Streams sampled for benthic macroinvertebrates in March 2017 in Tongariro National park, New Zealand, with respective FENZ† classes, order, width and altitude. Easting and Northing coordinates given in the New Zealand Transverse Mercator 2000 projection.

Nr.	Stream	Easting	Northing	FENZ class†	Order	Width (m)	Altitude (m)
1	Te Unuunuakapuateariki Stream	1820263	5631117	G1	4	3.8	713
2	Waitaiki Stream	1817009	5632207	A5	2	0.67	698
3	Mangawhero River	1809423	5636944	C8	4	6.2	675
4	Whakapapanui Stream d/s	1816846	5663864	G2	4	12	837
5	Makomiko Stream	1806498	5654459	G2	3	5.6	763
6	Whakapapanui Stream u/s	1819591	5656981	H1	3	5.2	1176
7	Mangaetoroa Stream	1804976	5642108	G2	3	5.2	748
8	Whakapapaiti Stream	1813564	5660873	G2	4	13.1	868
9	Mangatepopo Stream	1821783	5672549	C9	3	6.2	755
10	Te Whaiau Stream	1825556	5675020	C9	3	4.1	661
11	Whanganui River	1825204	5677982	C9	3	5.3	608
12	Poutu Stream	1841973	5671008	C9	2	7.4	520
13	Waihaha Stream	1842635	5660995	C9	3	6	679
14	Oturere Stream	1838209	5659395	C9	4	9.3	818
15	Mangatoetoenui Stream	1835725	5653608	G2	4	8.5	979
16	Waipakihi River tributary	1839751	5654006	G2	2	4.8	862

† Freshwater Ecosystems of New Zealand database (Leathwick et al., 2010)

3.2.3 Larval caddisflies

Sampling was conducted during March 2017. Five 0.1 m^2 Surber samples (250 μm mesh) were collected from riffles, haphazardly selected, within a ca. 25-m stream reach. Rare species were defined from the averaged abundances of those five samples. Species with limited distribution might be found in only a few microhabitats within a stream, thus sampling of all available microhabitats is required (Nijboer & Schmidt-Kloiber, 2004). Because of that, one kick-net sample was taken with a 30-cm opening, 250 μm mesh net for a period of 1 min from non-riffle habitats within the same 25-m stream reach; i.e. pools, stream margins, undercut banks, aquatic macrophytes, mosses. Samples were preserved in the field in 70% ethanol. All samples were sieved in the lab through a 500 μm mesh and identified to the lowest feasible taxonomic level using available keys (Smith & Ward, 2005; Winterbourn et al., 2006).

3.2.4 Adult caddisflies

Adult caddisflies were also collected during March 2017. A UV-light trap collected them actively and a Sea-Land-Air-Malaise (SLAM - Australian Entomological Supplies Pty Ltd, NSW, Australia) trap passively (Fig. 3.2). UV-light-traps consisted of a waterproof body which hosted a 12 V battery and timer, and two moveable arms screwed to its' sides with four UV-LEDs (peak wavelength: 395 nm). The timer was set to operate for four hours, starting just after sunset (approx. 19:30-23:30), and for one hour, just before dawn (approx. 05:30-06:30), when New Zealand caddisflies are most active (Ward et al., 1996; Collier et al., 1997). The trap was set inside a white, plastic tray (30 x 35x 5 cm), as close to the water as possible on the banks, or on flat boulders protruding above the water surface. Water was added in the tray, along with a few drops of detergent to break surface tension. One of the LED arms shed light on the water while the other lit the area in front of and over the trap and stream. Flying insects attracted to the trap were directed to the polarized light on the water surface and consequently trapped (Horvath & Kriska, 2008). Each trap operated in the field for one night, immediately after the end of the SLAM-trap sampling, so as not to interfere with the other trap's catch. One UV-light trap malfunctioned and thus 15 light-trap samples were collected. Identification was made to species or genus level (the latter usually for females), using the key of Smith (2014).

The SLAM-traps are a quadrilateral modified version of Malaise interception traps (Achterberg, 2009; Dodds et al., 2015). They were set on the stream banks, as close to the water as possible, while taking care that they were not covered by riparian vegetation. Positively phototactic insects are intercepted by the trap while flying and move towards the top of the trap where they fall in a collecting bottle with preservative liquid (e.g. 70% ethanol). To collect negatively phototactic species four white, plastic trays (30cm x 35cm x 5cm) were positioned horizontally, next to the trap's fabric. Water and a few drops of

detergent were added to these trays as well. They were left in the field for approximately 10 days. Twelve SLAM traps were spread across the sampled streams in the area, to cover all stream classes. Only three individuals were collected in the negatively phototactic traps and thus were not considered in the analyses. Identification was performed as for light-trap samples.

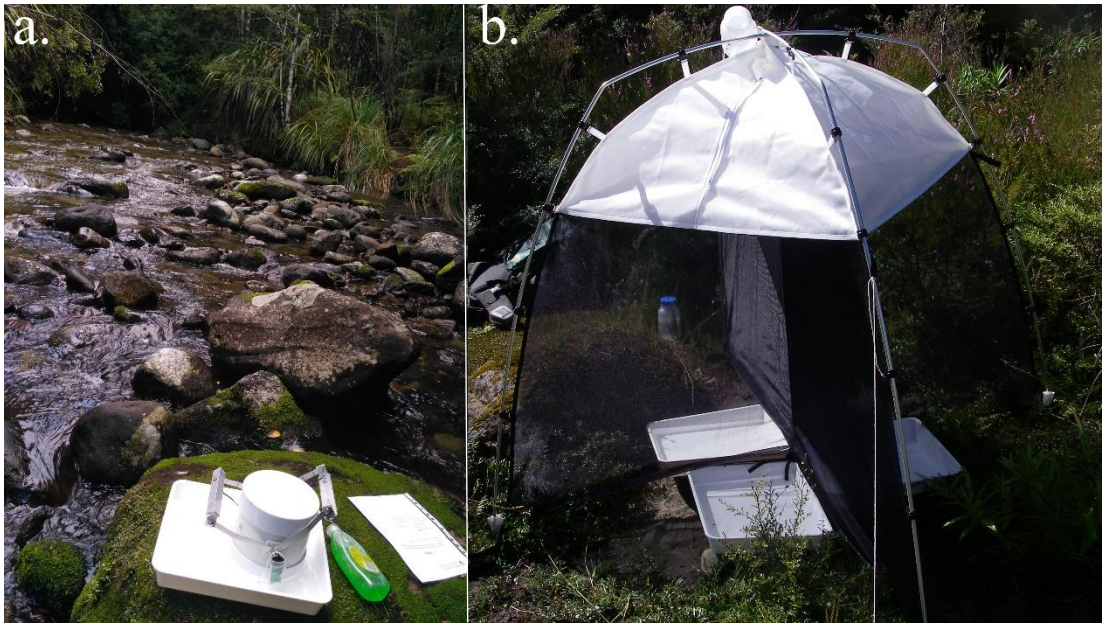

Figure 3.2: a) UV-light trap, Waihaha Stream and b) SLAM trap, Whakapapanui Stream, used to sample adult caddisflies in Tongariro National Park, New Zealand, March 2017.

3.2.5 Data analysis

Analyses were performed in R v.3.4.2 (R Core Team, 2020). Two datasets were analysed: i) caddisflies collected using all four methods, but with adult taxonomic level consolidated to that of the larvae; and ii) adult caddisflies sampled with the UV-light and SLAM traps identified to species level. Samples were compared separately for i) the benthic methods, ii) the traps and iii) all four methods together. Site nr. 2, Waitaiki Stream was right downstream from lake Rotokuru and hosted a radically different community

that masked the differences between the communities in the other streams and hindered analyses. Consequently, it was excluded from the final analyses.

Univariate metrics were calculated to describe the biodiversity of the community collected by each sampling method in terms of richness and diversity; taxa richness, effective number of taxa (i.e. the exponential of the Shannon diversity index, which weighs all species by their frequency, favouring neither common, nor rare), relative evenness as described by Pielou's J (Jost, 2010), percentage of rare taxa and individuals, using the package vegan (Oksanen et al., 2018). Usually, sampling is expected to underestimate true richness of a community because of missed rare species (Gotelli & Colwell, 2011; Chao & Chiu, 2016); therefore, the Chao1 richness estimator was also calculated for each method with the iNEXT package (Chao, 1984, 1987; Chao et al., 2014; Hsieh et al., 2016, 2018). Chao1 estimates the unseen/unsampled taxa by taking into account singletons (taxa with only one individual found in a sample) and doubletons (taxa with exactly two individuals found in a sample) (Chao & Chiu, 2016). However, non-parametric richness estimators such as Chao1 have been found to still underestimate true species richness in an ecosystem and should be better considered as lower bounds of richness (O'Hara, 2005). Sample-based rarefaction curves of taxonomic richness with 1000 runs were drawn to compare the efficacy of the different sampling methods in terms of species richness and sampling effort, as well as the estimated coverage of the biodiversity in the area by each method. Richness estimators and rarefaction curves have been shown to be biased when comparing richness in assemblages from different taxonomic groups (Cao et al., 2007). Thus, despite all focusing on aquatic insects, differences between benthic and trapping methods need to be interpreted more cautiously than differences among benthic and among trapping methods.

The number of shared taxa between the different methods was also calculated, as well as the number of taxa that were collected by only one method, to evaluate the redundancy in species inventory. To estimate the effect that unsampled species have on shared species and similarity estimators, EstimateS requires setting a number of individuals or samples, for a species to be considered rare. For these analyses the default limit of 10 individuals per sample was used.

Among-method differences in diversity and similarity metrics were evaluated using generalized linear mixed models (GLMM) with the method as a fixed effect and the sampled stream as a random factor, using the lme4 package (Bates et al., 2015). For count data (taxa richness) Poisson error distributions were used. For the other metrics, Gaussian error distribution. Using the package multcomp (Hothorn et al., 2017) pairwise comparisons between all four methods were performed and p-values generated, adjusted for multiplicity.

Taxonomic structure was analysed with the vegan package, using log(x+1) transformed abundances. Statistical significance of the differences among the community structure collected by the different methods was evaluated using Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001), with 9999 permutations, using Bray-Curtis distances. The communities were visualised in ordination space using non-metric multidimensional scaling (NMDS) with Bray-Curtis distances in two or three dimensions, to keep the configuration stress within acceptable limits. The compositional similarity of the communities was analysed through Procrustes analysis in the vegan package and tested with the function protest and 9999 permutations.

3.3 Results

3.3.1 Overall results

Sampling time differed greatly among the benthic and trapping methods. Both benthic sampling methods required less than an hour at each site, while light-traps required 5 hours for an overnight sampling and SLAM traps required approximately 10 full days. At the taxonomic level where larvae can be identified, 52 Trichopteran taxa were collected in total (Appendix B: Table S3.1); 40 from kick-net samples from 2201 individuals (8 unique taxa, not collected with any other method), 35 from Surber samples from 10189 individuals (5 unique taxa), 25 from UV-light traps from 1040 individuals (3 unique taxa) and 22 from SLAM traps from 1041 individuals (2 unique taxa). The benthic methods shared more taxa per sample than any other pair of methods, on average 10 from the total assemblages and five rare taxa (Appendix B: Table S3.2 and Fig. S3.1). From the benthic samples 27 taxa could be identified to species-level in kick-nets and 24 in Surbers. Using the adult caddisfly key, trap samples contained 44 species in total; 34 from the light traps and 27 from the SLAM traps. All taxa sampled with each method were considered rare in at least one sample based on our site-specific relative abundance criterion.

Among the sampled taxa that could be identified to species level, only four are "Naturally Uncommon", i.e. larvae of *Hydrochorema lyfordi,* and adults of *Hydrobiosis falcis* (also larvae), *Tiphobiosis cataractae* and *Paroxyethira hintoni*; the rest are "Not Threatened" (based on the New Zealand Threat Classification System criteria (Townsend et al., 2007; Grainger et al., 2018).

3.3.2 Larval sampling

Kick-nets collected on average 22% fewer taxa per stream than Surber samples, 14 and 18 taxa respectively (Tables 3.2 and S3.3; Fig. 3.3). Kick-net rare taxa richness (11 taxa)

was also lower than the Surbers' (15 taxa). When the estimated unsampled taxa were considered, numbers of total and rare taxa did not differ statistically between the methods, with 20 taxa on average in kick-nets and 22 in Surbers (16 and 19 were considered rare respectively). Thus, the difference between observed and estimated taxonomic richness was larger for the kick-net than the Surber samples. Kick-nets and Surbers did not differ with regards to the average percentage of rare taxa (76 and 86% respectively, Fig. 3.4A), and similarly when the unseen taxa were considered (81% and 88% respectively, Fig. 3.4B), or considering the percentage of individuals belonging to rare taxa (24% and 29% respectively, Fig. 3.4C). Taxonomic diversity (i.e. effective number of taxa) did not differ among the total communities (6.1 for kick-nets and 5.3 for Surbers), or their rare components (8.3 and 9.7 respectively) (Tables 3.2 and S3.3; Fig. 3.5A-B), and neither did the relative evenness of the total assemblages (0.7 and 0.6 respectively) (Fig. 3.5C).

Table 3.2 Biodiversity metrics calculated from stream macroinvertebrate samples collected with four sampling methods (Kick-nets, Surber samplers, UV-light traps, and SLAM traps), for the complete assemblages (Total) and their rare components (Rare). Samples were collected from 15 streams in the Tongariro National Park of New Zealand, March 2017.

	Total											
Biodiversity Metric†	Kick		Surber		UV-Light (c)		SLAM (c)		UV-Light		SLAM	
	Av.	SE	Av.	SE	Av.	SE	Av.	SE	Av.	SE	Av.	SE
NSp	13.9	1.11	17.9	0.80	9.0	0.94	5.8	1.24	9.9	1.07	6.3	1.45
Chao1 NSp	19.6	2.34	21.8	1.35	14.0	1.89	11.2	4.34	17.0	2.61	11.5	3.84
EfNSp	6.1	0.58	5.3	0.49	5.6	0.68	3.0	0.29	6.0	0.73	3.1	0.31
REv	0.7	0.02	0.6	0.03	0.8	0.05	0.8	0.06	0.8	0.05	0.8	0.06
Rare species %	76%	0.03	86%	0.02	86%	0.04	82%	0.07	88%	0.04	86%	0.05
Chao1 Rare species %	81%	0.02	88%	0.02	88%	0.05	86%	0.1	89%	0.05	89%	0.05
Rare individuals %	24%	0.03	29%	0.1	60%	0.1	58%	0.1	62%	0.10	59%	0.13
	Rare											
NSp	10.6	0.88	15.3	0.61	7.7	0.84	4.4	0.96	8.7	0.99	5.1	1.14
Chao1 NSp	16.3	2.20	19.3	1.28	12.7	1.99	9.9	4.18	15.8	2.71	10.2	3.61
EfNSp	8.3	0.61	9.7	0.51	6.1	0.72	3.7	0.71	6.8	0.81	4.3	0.91

† NSp = Number of species; Chao1 NSp = Chao1 species richness estimator; EfNSp = Effective number of species; REv = Relative evenness

Av = Average; SE = Standard Error; (c) = consolidated taxonomic level

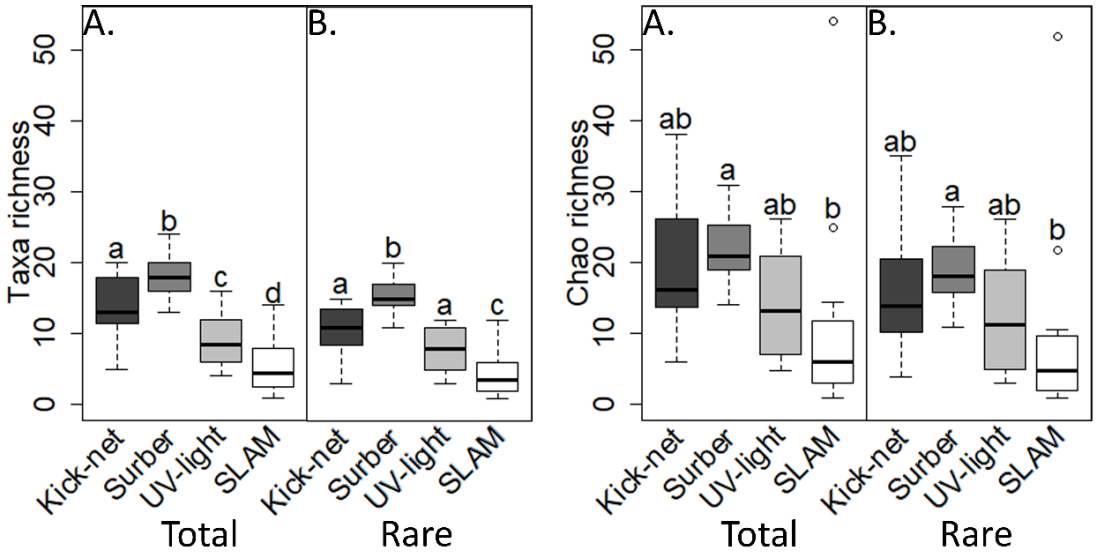

Figure 3.3: Observed taxa richness and Chao1 estimated richness for the (A) total assemblages and (B) their rare components, collected with kick-net samples, Surber samples, UV-light traps and Sea-Land-Air-Malaise traps, March 2017, in the Tongariro National Park, New Zealand. Methods in the same plot sharing a letter did not differ statistically based on GLMMs with site as a random factor (P>0.05).

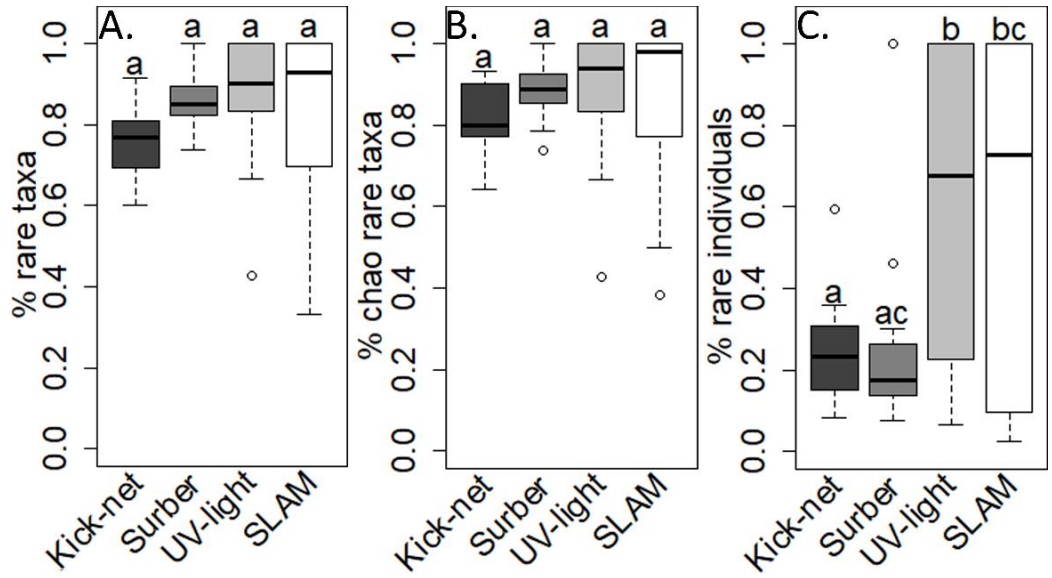

Figure 3.4: Percentage of rare taxa in terms of (A) observed and (B) estimated number of taxa, and (C) observed percentage of rare taxa in terms of number of individuals. Collected with kick-net samples, Surber samples, UV-light traps and Sea-Land-Air-Malaise traps, March 2017, in the Tongariro National Park, New Zealand. Methods in the same plot sharing a letter did not differ statistically based on GLMMs with site as a random factor (P>0.05).

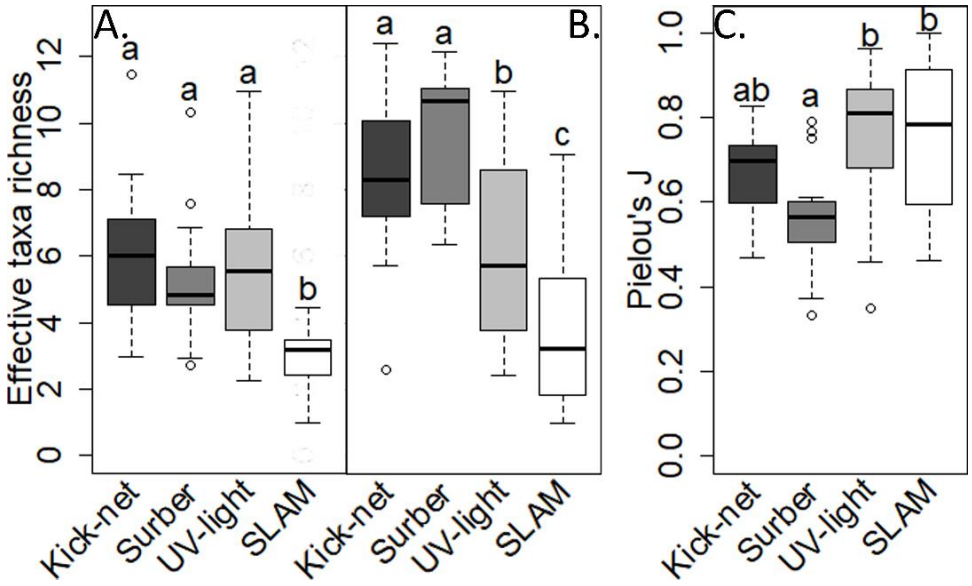

Figure 3.5: Effective taxa richness (exp(Shannon)) of (A) the total assemblages and (B) their rare components and (C) relative evenness (Pielou's J) of the total assemblages, collected with 15 kick-net samples, 15 Surber samples, 14 UV-light traps and 12 Sea-Land- Air-Malaise traps, March 2017, in the Tongariro National Park, New Zealand. Methods in the same plot sharing a letter do not differ statistically based on GLMMs with site as a random factor (P>0.05).

The rarefied taxa richness suggested that samples collected with the kick-net from non-riffle habitats in 15 streams described a richer community for a given sampling effort than did samples collected with Surbers from riffles (Fig. 3.6). Both methods were estimated to be relatively close to reaching an asymptote of taxa richness for additional sites sampled, with 45 taxa for kick-net samples and 38 for Surbers. However, kick-net samples were more variable, as indicated by the upper 95% confidence interval (CI) which reached 61 taxa, against 53 taxa for the Surber samples. This meant that a higher percentage of gamma diversity, i.e. the total taxonomic richness across the study area, can potentially be sampled with kick-nets as opposed to Surber samplers (Fig. 3.6).

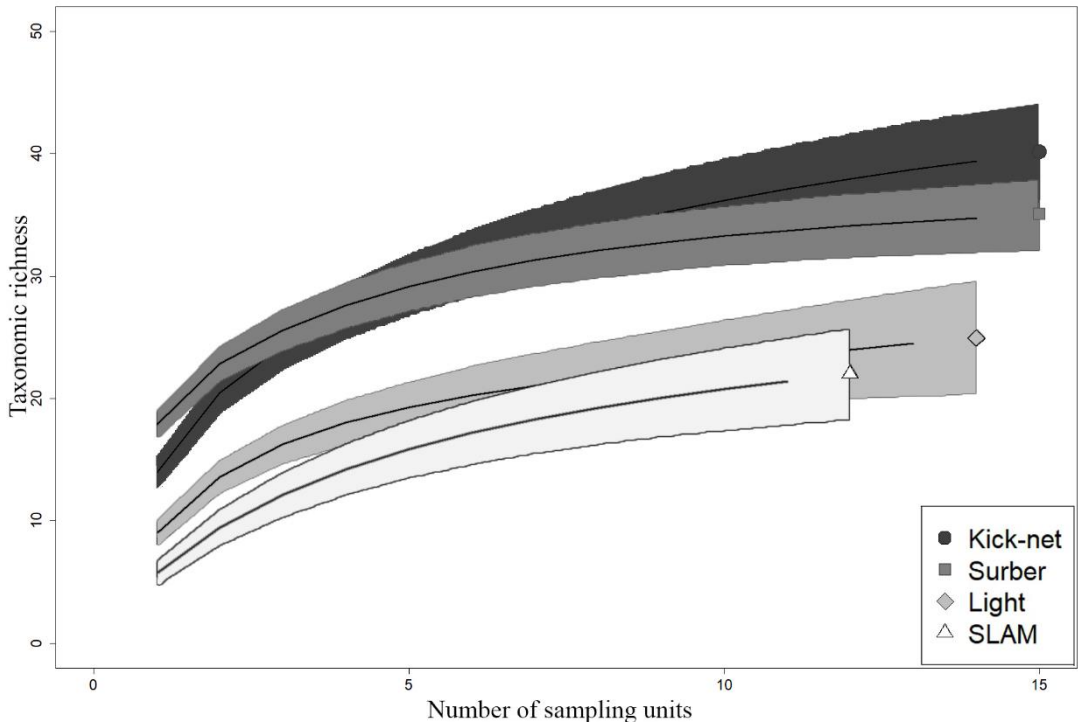

Figure 3.6: Rarefaction of species richness for kick-net, Surber, UV-light trap and Sea-Land-Air-Malaise trap samples, based on samples from 15, 15, 14 and 12 streams respectively, March 2017, in the Tongariro National Park, New Zealand. Upper & lower 95% confidence intervals indicated by the coloured areas.

Taxonomic composition of the total assemblages and the rare components differed significantly based on PERMANOVA (Table 3.3; Fig. 3.7). The ordinations of the total assemblages and their rare components revealed a stronger effect of the sampling method on community composition than the effect of the sampled stream. The ordinations of total assemblages were correlated (r=0.66, P=0.002), but not of the rare component (r=0.36, P=0.33). Kick-net samples were more variable than Surber samples for both the complete samples and their rare components, with the difference being wider for the latter.

Table 3.3: Pairwise PERMANOVA with 9999 permutations, assessing the statistical significance of differences in the structure of the total assemblages and their rare components, from samples collected in 15 streams, with four sampling methods, in the Tongariro National Park, New Zealand, in March 2007.

	All taxa			Rare taxa		
	$F_{(df)}$	adj.R^2	Pr(>F)	$F_{(df)}$	adj.R^2	Pr(>F)
Kick-Surber	$7.52_{(1,29)}$	0.21	**<0.001*****	$3.77_{(1,29)}$	0.12	**<0.001*****
Light-SLAM	$7.09_{(1,25)}$	0.23	**<0.001*****	$3.39_{(1,25)}$	0.12	**<0.001*****
Kick-Light	$12.24_{(1,28)}$	0.32	**<0.001*****	$6.36_{(1,28)}$	0.19	**<0.001*****
Surber-Light	$14.3_{(1,28)}$	0.35	**<0.001*****	$9.65_{(1,28)}$	0.26	**<0.001*****
Kick-SLAM	$5.85_{(1,26)}$	0.19	**<0.001*****	$3.97_{(1,26)}$	0.14	**<0.001*****
Surber-SLAM	$8.96_{(1,26)}$	0.26	**<0.001*****	$7.79_{(1,26)}$	0.24	**<0.001*****

Significance level: *** < 0.001

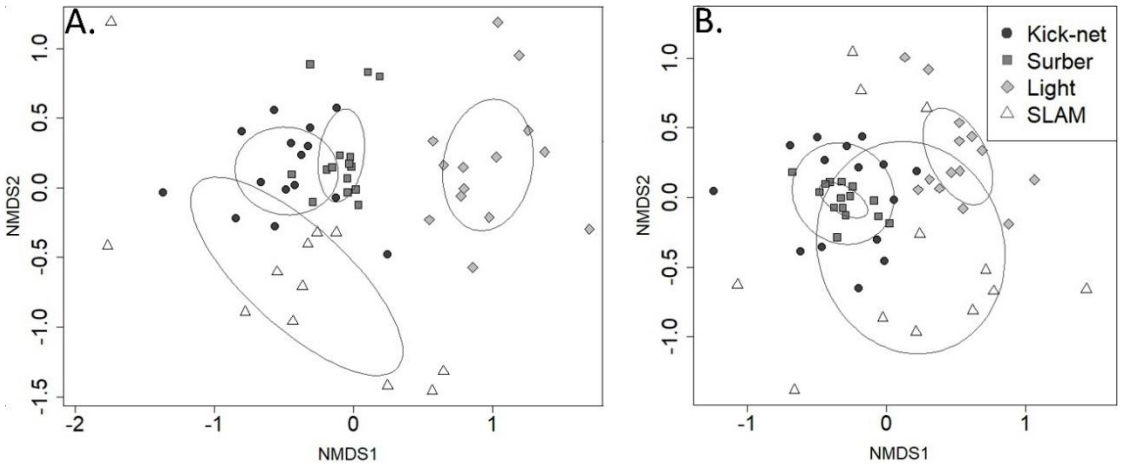

Figure 3.7: NMDS of log(x+1) transformed absolute abundance samples of (A) the total Trichopteran assemblages and (B) their rare components, collected in 15 kick-net samples, 15 Surber samples, 14 UV-light traps and 12 SLAM traps, March 2017, in the Tongariro National Park, New Zealand.

3.3.3 Adult sampling

UV-light traps collected on average 33% more species than SLAM traps, 10 and 6 species respectively (Tables 3.2 and S3.3). Out of these, 45% more species were considered rare in the light than in the SLAM traps, on average 9 and 5 species respectively. When the estimated unsampled species were considered, the average number of species in the light trap samples increased to 17, but was not statistically higher than the SLAM traps that

rose to 12. Similarly, the percentages of rare species, estimated rare species and rare individuals did not differ between the two methods.

Light trap samples were on average twice as diverse as SLAM trap samples for the total assemblages, while the rare components of the light trap samples were on average 37% more diverse (Table 3.2 and S3.3). Relative evenness of the total assemblages from both traps was on average 0.8.

The rarefied species richness suggested that the UV-light traps collected a slightly richer Trichopteran community for a given number of streams samples than did the SLAM traps (Fig. 3.6). This difference was more pronounced with low numbers of sampled streams, while the SLAM trap samples gained ground with increasing number of samples. UV-light trap samples with species-level data were found to be very variable and far from reaching an asymptote; the estimated asymptotic species richness (101 species) and the upper 95% CI (443 species) are indicative of the variability of these samples. SLAM traps on the other hand were shown to be close to collecting the maximum gamma diversity they could sample (32 species and 50 species at the upper 95% CI). Similar patterns were observed for the consolidated taxonomic level assemblages (UV-light traps: asymptotic richness 48 taxa, upper 95% CI 180 taxa – SLAM traps: asymptotic richness 28 taxa, upper 95% CI 51 taxa) and thus the graph based on the species-level data is not presented.

Species composition differed significantly between the two types of traps based on PERMANOVA, for both the total assemblages and their rare components (Table 3.3). The ordinations of the total assemblages (stress: 0.15) were shown to be marginally non-significantly correlated ($r=0.58$, $P=0.054$), while their rare components (stress: 0.17) were not correlated ($r=0.43$, $P=0.3$). SLAM-trap samples were more variable than the light-trap samples, more so for the rare components.

3.3.4 Benthic larval vs aerial adult sampling

When the taxonomic level of the adult individuals was consolidated with that of the benthic larvae, the benthic sampling methods collected on average between 30% and 67% more taxa than the traps (Fig. 3.3; Tables 3.2 and S3.3). Similar differences were found for the rare components, with the benthic methods collecting on average between 47% and 73% more than the traps, except for the comparison between kick-nets and light traps which did not differ significantly. After considering the estimated number of unsampled taxa, only the Surber assemblages differed from the SLAM traps, with the former estimated to collect 51% more taxa than the latter. The same patterns were observed for the rare components. The percentages of observed and estimated rare species did not differ significantly between benthic and aerial methods (Tables 3.2 and S3.3; Fig. 3.4). However, the percentage of rare individuals in the trap samples was on average 57%, higher than the less than 30% of the benthic samples. Only the percentages of rare individuals in Surbers and the SLAMs did not differ. The caddisflies of the latter were almost all considered rare.

SLAM samples were the least diverse, with an average effective number of species of 3, while light trap samples had 6. The latter did not differ significantly from the benthic methods (Fig. 3.5a; Tables 3.2 and S3.3). The differences were more pronounced between the rare components. The trap samples (6 and 4 for light and SLAM traps respectively) were less diverse than the benthic samples (8 and 11 for kick-nets and Surbers respectively) (Fig. 3.5b; Tables 3.2 and S3.3). Surber samples collected the most uneven assemblages with an average value of 0.56, while the other methods ranged between 0.7 and 0.8 (Fig. 3.5c; Tables 3.2 and S3.3).

Rarefaction of taxa richness suggested that the benthic sampling methods are clearly more effective than the adult trapping methods for a given number of sampled

streams with regards to the consolidated taxonomic level data (Fig. 3.6). This difference was minimised but still not reversed, when the species-level data of the trap samples were considered opposite the higher level data of the benthic samples.

All assemblages were clearly different (stress: 0.19 for total and 0.22 for rare - Fig. 7a) and their compositions statistically different and the same pattern was observed for their rare components (Table 3.3; Fig. 3.7b). Only the assemblages collected by Surbers were correlated with the ones from the light traps (r=0.62, P=0.003) and the rare component of the Surbers were correlated with the rare components of the SLAM traps (r=0.59, P=0.03).

3.4 Discussion

How to manage and/or monitor rare invertebrate species is extremely challenging, particularly if multiple species need to be monitored simultaneously (Karr, 1999). However, given the rate at which species extinctions are currently occurring on the planet it is critically important, especially as less resources seem to be available for such activities (Pimm et al., 2014; Ceballos et al., 2015). In this study we evaluated the ability of four sampling techniques (kick-nets, Surber samplers, UV-light traps and SLAM traps) to quantify rare, lotic macroinvertebrates in New Zealand streams. As targeting and finding rare species can be difficult because of their low occurrence probability, rare taxa were defined as those with relative abundance equal to or lower than 0.5% or 10 individuals in their respective communities (Colwell, 2013; Sgarbi & Melo, 2018). This led to all taxa collected with all methods being considered rare in at least one site. This might be related to the spatiotemporal scale of the study. In small scales (e.g. in a single stream, on a single occasion or within a small drainage basin) populations can fluctuate naturally. A single, active sample is a snapshot in space and/or time, while a passive

sample can incorporate a greater period and/or area (Turner & Trexler, 1997). This in turn presents challenges for species conservation as work will be required at different scales, depending on the factors driving rarity and/or extinction risk (Hartley & Kunin, 2003).

The analysis of the benthic samples suggests that, in a single stream, Surbers can collect a clearly differentiated and taxonomically richer community from riffles, than kick-nets from non-riffle habitats. Surbers are most often used for stream biomonitoring in riffles, as those habitats host more species sensitive to pollution (Rosenberg & Resh, 1993; Stark et al., 2001; Friberg et al., 2011) and can provide density estimates of the macroinvertebrate community. Yet the threats that freshwater ecosystems face are not limited to pollution (Dudgeon et al., 2006; Reid et al., 2018) and the community changes they might evoke are, thus, not bound to be detected in riffle-inhabiting assemblages (Stark et al., 2001). Kick-net samples in this study came from non-riffle habitats and still collected about 80% of the taxa collected in Surber samples in each stream (these methods shared the most taxa in their samples) and in total 12% more taxa for the whole area, 11 of which were not collected by the Surbers. Furthermore, the abundances of the taxa collected with the Surbers were, as per typical monitoring protocols in New Zealand, averaged over five samples in each site (five one-minute Surber samples), in comparison to the one-minute kick-net. Consequently, Surber samples required processing of a much higher number of individuals to describe local diversity to that extent.

The absence of significant differences between the biodiversity metrics of communities collected with the benthic methods, may be explained by the structural variability of non-riffle macrohabitats that were sampled with kick-nets (Baillie et al., 2019) and the relatively high diversity of taxa that are expected to be present in riffles of unimpacted streams (Allan & Castillo, 2007; Stark et al., 2001).

Both methods appeared to be similarly effective in sampling gamma diversity, with the kick-nets having slightly higher potential. This, in combination with the higher total number of sampled taxa, higher number of unique taxa, higher estimated undetected taxa for kick-net samples and moderately strong correlation between the assemblages sampled by these methods could imply that a standardized kick-net, proportional habitat-sampling protocol that would also cover riffle habitats, would be the best option for monitoring the assemblages of lotic caddisfly larvae. Another option would be, as in this study, sampling with both methods in different microhabitats, but this would require increased sampling and processing effort, while it would limit the range of analyses that can be performed in a merged dataset comprising data collected by different methods.

Analysis of the adult caddisfly samples suggests that the UV-light traps are slightly more effective in describing the species composition in an area, with regards to the number and diversity of the species they collect. These differences, along with clear distinction between the assemblages' composition, can be attributed to the differing trap set ups. The UV-light traps are highly selective for UV-sensitive species, or even particular sexes (Southwood & Henderson, 2000) and can attract individuals from different habitats or away from the sampling location (Gerecke et al., 2007). SLAM traps with only the top collector are also selective for positively phototactic species, but do not attract them, rather they passively collect them if they fly on to the fabric (Southwood & Henderson, 2000; Achterberg, 2009). If there is a bottom collector included, they can be unselective. However, they are more difficult to set properly near the stream. They require larger space than the light traps and trees to be tied to or ground suitable for pegging, in order to be secure against wind or flow disturbance (Winterbourn, 1997). If a bottom collector design such as this study's is used, they also require a flat surface. Their trapping area is only about 3.2 m^2 (Dodds et al., 2015), smaller than the attraction area of the UV-

light traps, although this depends on the UV-light's brightness and wavelength, and can be limited by the surrounding vegetation (Pohe et al., 2018). Other options for the SLAM traps would be to hang them from the canopy, or let them float on the water (Skvarla & Dowling, 2017). Both traps require extensive sampling to ensure that a representative sample of each community will be collected (Collier et al., 1997) and revisiting the sampling site. UV-light traps can collect an adequate sample overnight, or even within a few hours, during the peak activity of the target community. SLAM traps require several days to collect a useful sample. The relatively low numbers of individuals collected from some of the traps might be related to low temperatures or overnight rain and/or wind in the area during that time of the year. These can have a big effect on both single-night light trap samples and multi-night SLAM trap samples (Collier & Smith, 1998).

The SLAM trap samples' species accumulation curve suggested that this method reached very high coverage for the Trichopteran assemblage. However, as indicated by the benthic samples and the light trap samples this was considerably smaller than the actual number of species living in the area. SLAM traps should be able to sample every species flying along the riverbanks. This result is most probably a product of the variability created by the particular trap set-up requirements and the local habitat conditions. UV-light traps on the other hand would require a major increase in the number of sampled streams in order to maximise sampled richness of species attracted by UV-light. However, they would still not be able to fully sample gamma diversity in the area, as the non-polarotactic species would not be attracted. They do trap species that do not live in shallow riffles and are not sampled by the usual benthic sampling methods or do not live in lotic systems at all, such as lakes, ponds and seepages (e.g. *Tiphobiosis sp*.). This can enrich the sampled species pool, but these assemblages might not be inextricably linked to the studied ecosystems. However, the limited sampling time (one night) in

combination with the low temperatures would probably not allow for large numbers of vagrant individuals to be attracted by the UV-light. A negative aspect of light-trapping in conservation studies, is that when a polarotactic species is also of conservation concern, they can have detrimental side-effects on the local population, by killing too many individuals from a wide area, while the other methods have more localized effects. Finally, SLAM traps, and to a lesser extent light traps, can collect considerable by-catch of terrestrial insects (Pohe et al., 2018).

As expected, the traps collected more taxa that could be identified to species level, because adult caddisflies are more easily identified to that level than larvae (Smith, 2014). However, on average, more taxa were collected with the benthic methods and their rare components were more diverse. Even when the taxonomic level of the adults was kept at the species level, the traps did not collect more species than the benthic methods. This result contrasted our expectations and other studies' results, where species richness from adult insect assemblages was higher than the taxonomic richness from benthic samples (Houghton et al., 2011). Trap efficacy depends on the timing of sampling more than the benthic sampling methods. Insect flying activity can be highly seasonal, diurnal and weather dependent (Southwood & Henderson, 2000). Benthic invertebrates are available for most of the year, although they can be flushed away during flooding events and then require a certain time to recolonise the substrate and reach a natural dynamic equilibrium (Scarsbrook, 2000). Sampling effort differs radically between benthic and trapping methods. Benthic methods require less time in the field (a few minutes for either of them) and much longer sample-processing time in the lab, while the traps in this study required double visits and 5 hours and about 10 full days for light and SLAM traps respectively, with much less time in the lab. The higher richness observed in benthic samples resulted possibly from the larger number of collected individuals. However, in relative terms, the

traps sampled greater richness with fewer individuals, thus being more effective and less environmentally damaging.

This study demonstrates the strengths and weaknesses of each of four sampling methods (kick-net, Surber sampler, UV-light trap and Sea-Land-Air-Malaise trap) and considers how can they be used best in stream macroinvertebrate biodiversity studies (Table 3.4). Species inventorying will benefit mostly from a combination of benthic and adult trapping methods, since each of them takes advantage of different elements of the species biology and collects species the other methods may miss. If the available funding allows for multiple expeditions across a longer time period, then possibly a combination of adult trapping methods will be more advantageous, since with fewer numbers of individuals a more precise species-level inventory could be constructed. UV-light and SLAM traps collect very different assemblages and each collects species not collected by the other or by the benthic methods, but considering efficiency, effort and cost, UV-light traps seem to be a preferable option. If the purpose is to monitor species population sizes, then more standardized methods are necessary, and the benthic samples will be more appropriate. Surbers from riffle habitats appeared to collect a richer assemblage of Trichoptera than kick-nets from non-riffle habitats, but the latter has greater potential with a proportional habitat sampling protocol that will include riffle habitats as well. The adult caddisfly assemblages did correlate with the larval assemblages, but not strongly enough to show a direct interchangeability. Alternatives, such as the combination of benthic assemblages and DNA metabarcoding technology, might be able to give a more accurate and useful description of the stream macroinvertebrate community (Elbrecht & Leese, 2015; Elbrecht et al., 2017). Documenting biodiversity in an area will require the use of as many methods as possible, to take advantage of each method's strengths and reduce the effects of each method's weaknesses.

Table 3.4: Factors affecting collection of benthic caddisflies (also applicable to other macroinvertebrate taxa) by kick-nets and Surber samplers, and collection of adult caddisflies (also applicable to other insect taxa) by UV-light and Sea-Land-Air-Malaise (SLAM) traps

	Kick-nets	Surbers	UV-light trap	SLAM trap
Sampling difficulty	Easy	Easy	Easy set-up	Difficult set-up
Sampling area size	Variable - protocol dependent	Fixed - quadrat	Variable - riparian habitat dependent	Fixed - trap fabric area
Habitat specificity	Flexible	Specific - run/riffle	Flexible	Flexible
Sampling duration	Short (minutes)	Short (minutes)	Medium (hours)	Long (days)
Field visits required	Single	Single	Double	Double or more
Local environment effects on the catch	Flooding	Flooding	Temperature, Wind	Temperature, Wind, Vegetation, Distance from stream
Diurnal variation	Low	Low	High	High
Sampled taxa selectivity	Non-selective	Non-selective	Selective - positively polarotactic insects	Selective - positively polarotactic insects if only top collector is used
Vagrant taxa collection possibility	Low	Low	High	Low
Terrestrial by-catch	Low	Low	High	High
Sample processing effort in the lab	High	High	Low	Low
Taxonomic level identification	High - Coarse	High - Coarse	Low - Species	Low - Species
Quantitative/Qualitative data	Qualitative - semi-quantitative	Quantitative	Qualitative	Qualitative
Number of species over number of individuals ratio	Low	Low	High	High

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Chapter 4

Are the common and rare components of stream macroinvertebrate communities related to the same local environment characteristics?

Abstract

Rare species comprise a large component of natural communities' species richness but are often excluded from analyses as they supposedly do not follow consistent ecological patterns. Their exclusion can, however, confound the discovery of links between communities and the environment, as their rarity status might actually be related to environmental factors, which are not related to the common components of the communities. We investigated the relationships between local-scale environmental variables and the common, rare and total (common + rare) taxonomic components of benthic stream invertebrate communities. We also assessed adult Trichoptera assemblages, which offer finer taxonomic resolution, useful for detecting rare species. We collected benthic Surber samples and adult caddisflies with UV-light traps from 15 streams in the Tongariro National Park, Aotearoa New Zealand. Rare taxa were defined as those with abundance equal to or less than 10 individuals or 0.5% of the total abundance at each site. Biodiversity metrics of the benthic components were related to similar sets of environmental variables, only differing in relationship strength. Inclusion of rare taxa weakened the link between assemblage structure and potential environmental drivers but improved the correlation of environmental variables' and the community's ordinations. Benthic Trichoptera biodiversity metrics were also linked to the same variables for rare and common assemblages. The total communities were linked to the same variables but inversely, potentially because of niche correlation among taxa and clear habitat preferences distinguishing common and rare taxa. Multivariate correlations with environment variables improved with the inclusion of rare taxa. Selection of the most important environmental variables improved the ordinations' correlations, with the biggest improvement seen for the rare components. The relationships between adult caddisfly assemblages and environmental variables were mostly driven by the rare

components, as the common components were limited because of the sampling timing and rarity definition. Rare taxa were found to carry complementary information to that of the common ones and facilitate or even determine discovery of relationships between stream macroinvertebrate communities and local environmental factors.

4.1 Introduction

Communities comprise a few very abundant species and many rare ones (Gaston, 1994; Nijboer & Schmidt-Kloiber, 2004; Williams, 1944). This is important in light of the global decline of ecosystems and species extinctions, often termed "the sixth mass extinction" (Barnosky et al., 2012) and the effect rarity can have on these changes (Hull et al., 2015). Despite this apparent "commonness of rarity", studying rare taxa assemblages is challenging. The definition of rarity is arbitrary (Gaston, 1994; McCreadie & Adler, 2008) and can depend on absolute/relative abundance, range and/or habitat specificity (Chapter 1). Locally rare species might be common elsewhere (Carney, 1997), and can be difficult to sample representatively, complicating their incorporation in community studies and may even result in their exclusion (Cao et al., 1998). They can be missed by subsampling protocols (Cao et al., 1998; Vermeij & Grosberg, 2018), creating sparse community matrices (Gauch & Gauch, 1982), and hindering the interpretation of abundant species' patterns (Marchant, 2002). Nevertheless, in an age when rare species are becoming rarer, their innate value and potential contribution to ecosystem function and services warrant their conservation (Cardinale et al., 2004).

Rare species are common in freshwater ecosystems as well (Cao et al., 2001). As in wider ecology, it remains unclear whether they should be included in data analysis (Cao et al., 1998, 2001; Cao & Williams, 1999; Marchant, 1999, 2002). Rare species are commonly deleted from multivariate analyses as outliers, statistical nuisance and/or containing redundant information (Cao et al., 1998; Hawkins & Norris, 2000; Marchant, 1999, 2002; Roden et al., 2018), even though data on common taxa can also be noisy (Arscott et al. 2006). Subsampling or identification to a higher taxonomic level (e.g. for early instar larvae) might exclude rare species from samples (Nijboer & Schmidt-Kloiber, 2004; Winterbourn et al., 2006). These issues can hinder detection of subtle gradients,

important for conservation planning (Cao et al., 2001; Faith & Norris, 1989). Flying adults have been proposed as a supplementary source of information about the structure of aquatic communities (Joy & Death, 2013; Valente-Neto et al., 2016), because of the greater ease to identify them to species level (Smith, 2014) and the more detailed dataset they can provide.

Identifying the causes and drivers of rarity is a daunting task (Gaston, 1994). Species-specific causes may be demographic characteristics, dispersal abilities, range, habitat preference and biotic interactions (Cao et al., 2001; Lennon et al., 2004; McCreadie & Adler, 2008; Schmidt-Kloiber & Nijboer, 2004). Common species are often considered to be abundant and/or widespread generalists exploiting a variety of resources, while specialist rare species exploit only specific resources (Gaston, 1994; McCreadie & Adler, 2008). Rare species may prefer marginal habitats that are characterised by rare sets of environmental conditions and will not benefit from additional space or resources (Chapman, 1999). However, such patterns are not universal and depend on the specific type of rarity considered, obscuring the interpretation of observed patterns (Gaston, 1994; McCreadie & Adler, 2008; Spitale, 2012). For example, Chapman (1999) suggested geographically rare invertebrates can be habitat generalists, and Arscott et al. (2006) suggested ubiquitous taxa with low abundances might be sensitive to specific types of disturbance.

A multitude of, often interacting, environmental factors have been found to drive the composition and diversity of benthic macroinvertebrates' assemblages (Santoul et al., 2005; Vinson & Hawkins, 1998). At the catchment scale, the size of the area drained by a stream and the dominant biomes and types of land-use within its limits can exert an overarching effect on stream communities (Allan, 2004; Harding et al., 1998; Hawkins et al., 2000; Vinson & Hawkins, 1998). The study scale can affect the patterns identified, as

communities have often been found to be structured by local rather than regional factors (Death & Joy, 2004; Norris, 1995). Focusing on separate stream reaches, altitude, width and depth of the reach, which change along the stream network similarly lead to communities changing along the network (Brooks et al., 2005; Hawkins et al., 2000). Environmental characteristics relevant to the abundance of resources (primary productivity, canopy cover, disturbance) or the presence of predators can determine the species present and the sizes of their populations (Canning et al., 2019; Death & Joy, 2004; French & McCauley, 2018; Hauer & Lamberti, 2011; Huttunen et al., 2017; Lorenz & Wolter, 2019; Tonkin et al., 2013; Tonkin, 2014). Within a given stream, community structure can change with the physicochemical characteristics of the water-column, such as velocity, flow, temperature, conductivity and dissolved oxygen (Brooks et al., 2005; Hawkins et al., 2000; Jacobsen et al., 1997; Lorenz & Wolter, 2019; Quinn & Hickey, 1990a, b; Sarremejane et al., 2018; Tonkin & Death, 2012; Vinson & Hawkins, 1998). Finally, the macroinvertebrates' movements and establishment in an area can be affected by fine details in the space they actually inhabit, the stream substrate, such as substrate roughness, size and stability (Brooks et al., 2005; Faith & Norris, 1989; Lorenz & Wolter, 2019; Schwendel et al., 2011; Vinson & Hawkins, 1998), and also sedimentation and debris jams (Baillie et al., 2019; Hawkins et al., 2000).

Rare species richness is often associated with diverse habitats such as aquatic vegetation and debris jams (Baillie et al., 2019; Jenkins et al., 1984; McCreadie & Adler, 2008) and even muddy substrates, despite the last not being characteristic of natural streams (Nijboer & Schmidt-Kloiber, 2004). Habitat patch size can render regionally rare species, locally common (Chapman, 1999), while hydrogeomorphology and water chemistry have been linked to rare assemblages' structure (Jenkins et al., 1984; Faith & Norris, 1989). Disturbance is thought to disproportionately affect rare species, as small

populations are more prone to local extinction, but they can be more resistant to some kinds of disturbance (e.g. logging) than common species (Hawkins et al., 2000). Resilient generalists with naturally low abundance can take advantage of reduced flows, while common generalists or rare specialists with limited distribution require higher flows and unpolluted waters (Clarke & Murphy, 2006; Nijboer & Schmidt-Kloiber, 2004; Sarremejane et al., 2018).

Whether the common and rare components of benthic macroinvertebrate communities respond differently to their local environment, and whether there is an advantage in combining them in analyses, remains unclear. Furthermore, the existence of parallel patterns between the relationships of benthic and adult aquatic insect communities with their local environment has also not been adequately evaluated (Joy & Death, 2013). This study explored the local-scale environmental factors driving the structure of the i) rare, ii) common and iii) total (rare + common) taxonomic components of benthic and flying stream invertebrate communities in a pristine area without strong environmental gradients and anthropogenic stressors.

4.2 Materials & Methods

4.2.1 Study area

Study streams are located in the Tongariro National Park, in the central North Island of Aotearoa New Zealand, which is mostly unimpacted by human activity. It is dominated by the central volcanic massif (CVM - consisting of the mountains Ruapehu, Ngauruhoe & Tongariro) and the Tihia-kakaramea volcanic massif to the north, both comprised of andesitic rocks. The presence of the CVM affects the distribution of rainfall around the national park by casting a rain-shadow on the south and east sides, which receive about 1,100 mm/year, while the north and west sides can receive up to three times that amount.

This results in larger areas of bare ground to the east, while on the rest of the park plant communities vary from broadleaf- and mixed beech-podocarp, to exotic *Pinus radiata* plantations, native tussock and scrubland (Tonkin et al., 2013).

To determine the appropriate number of streams for a representative taxonomic inventory, we evaluated benthic macroinvertebrate data collected with Surber samplers, from 47 streams in the Park, by Tonkin et al. (2013). Using EstimateS 9.1.0 software (Colwell, 2013) we randomly resampled those streams until no more than one taxon was added to the total taxonomic pool of the area for an additional stream sampled. The small benefits of a slightly longer taxonomic inventory would be heavily overshadowed by a linear increase in sampling effort. We repeated this 100 times. This analysis suggested 16 was the ideal number of streams to sample for this region. We selected 16 streams from all potential streams in the national park in proportion to stream type, based on the Freshwater Ecosystems of New Zealand database (FENZ – Leathwick et al., 2010) level 2 classification, which distinguishes 100 classes (Fig. 3.1 and 4.1). The six most abundant classes in the park were sampled (Table 3.1). Streams were distributed around the park and were also selected for accessibility. Sampling sites were located between 520 and 1180 m a.s.l. (mean = 778m). Classes C9 and G2 were the most abundant and are characterized by moderate to low, stable flow. Landcover was mostly characterized by native shrubs and forest. Mature exotic forest plantations were found in only three sites (Te Unuunuakapuateariki, Te Whaiau & Poutu streams), where they comprised 30-40% of the riparian zone. However, benthic communities in exotic forest streams in Aotearoa New Zealand have been found to closely resemble communities in streams running through native forests (Quinn et al., 1997, 2004).

Figure 4.1: Representative streams of the two most common FENZ classes in the Tongariro National Park, New Zealand: a) C9 class stream (Otutere) and b) G2 class stream (Makomiko) with UV-light trap. Benthic macroinvertebrates and adult caddisflies were sampled in March 2017.

4.2.2 Definition of rarity

There are many ways to define rarity (Gaston, 1994; Rabinowitz, 1981). We considered taxa to be rare when their abundance was equal to or less than 0.5% of the total abundance at each site, or (for samples with less than 200 individuals, where 0.5% of the total abundance was less than one individual) equal to or less than 10 individuals. While not considering the vulnerability of different species, such criteria are often used when species are discarded from analyses for the sake of "noise" reduction in data analysis (Sgarbi & Melo, 2018; Yu et al., 2017).

4.2.3 Benthic macroinvertebrates

Sampling took place in March 2017. Five 0.1 m^2 Surber samples (250 µm mesh) were taken from riffles, haphazardly selected, within a ca. 25 – 50 m reach of each stream. Samples were preserved in the field in 70% ethanol. All samples were sieved in the lab through a 500 µm mesh and identified to the lowest feasible taxonomic level using

available keys (McLellan, 1999; Smith & Ward, 2005; Towns & Peters, 1996; Winterbourn et al., 2006). Where identification to a described, lower taxonomic level was not possible, individuals were classified into morphospecies, based on habitus characteristics, i.e. their general appearance. We averaged the abundance of each taxon over the five samples collected in each site and used these averages to define rare species for the different assemblages; the total insect assemblage (hereafter TIA), the common (CIA) and the rare (RIA).

4.2.4 Adult caddisflies

Adult caddisflies were also collected during March 2017, with a UV-light trap. The trap design consisted of a waterproof body placed inside a white, plastic tray (30 x 35x 5 cm). The body hosted a 12V battery and timer inside, and two moveable arms screwed to the sides with four UV-LEDs each (peak wavelength: 395 nm). The timer turned the LED-lights on for four hours after sunset (approx. 19:30-23:30) and for one hour before sunrise (approx. 05:30-06:30), during which periods Aotearoa New Zealand caddisfly activity is at its peak (Collier et al., 1997; Ward et al., 1996). The trap was set as close to the water as possible. Water was added in the tray, along with a few drops of detergent to break surface tension. One of the LED arms faced the water in the tray and the other the area over and in front of the trap, up- or downstream. Positively polarotactic adult insects were attracted by the polarized light to the water surface (Horvath & Kriska, 2008). Each trap operated for one night. One UV-light trap malfunctioned (site nr. 16, Waipakihi stream) and thus 15 light-trap samples were collected. Identification was made to species or genus level (usually for females), using the key of Smith (2014). The total caddisfly assemblages are indicated as TCA, and the common and rare components as CCA and RCA respectively.

4.2.5 Local environmental factors

We measured multiple biotic and abiotic factors describing the local environment, which are related to benthic lotic macroinvertebrates and are often used in freshwater studies. Some of those are related to the adult aquatic insects as well, for which we also measured additional factors.

4.2.5.1 Aquatic flora measurement

We assessed periphyton biomass by measuring chlorophyll a from five stones at each site, collected haphazardly from riffles within the sampling reach and kept on ice in the dark until processed. We extracted chlorophyll a by leaving the stones in 90% acetone, at 5 ^{o}C, for 24 h, in the dark. Absorbances were read at 750, 665 and 664 nm on a Varian Cary 50 conc UV-Visible Spectophotometer (Varian Australia Pty Ltd, Mulgrave, Australia) and were converted to pigment concentration following Steinman et al. (2007). We calculated stone surface area following Graham et al. (1988), which we halved because only half of the stone surface is available for periphyton growth (mean upper stone surface area = 22 cm^2).

Visual assessment of periphyton cover has also been shown to be a reliable method for periphyton biomass assessment (Kilroy et al., 2013; Tonkin et al., 2014). We distinguished four categories and estimated percentage of; bare (no cover), thin films (0-1 mm), mats (>1 mm) and filamentous algae. Bryophyte and macrophyte cover within the sampling reach were assessed on a qualitative scale (0=none, 1=rare, 2=moderately abundant, 3=abundant).

4.2.5.2 Physicochemical sampling

We assessed the abiotic environment at the same time as the macroinvertebrate sampling (Table 4.1). We measured width, depth, velocity, percentage of canopy cover and assessed coarse particulate organic material (CPOM) cover visually at each sampled riffle. We estimated the percentage of canopy cover with a spherical convex densiometer (Forestry Suppliers, Inc.), by multiplying the number of squares on its surface (max = 24) that were reflecting vegetation by 4.17. To assess velocity, we used a velocity head rod and measured the water depth and the super-elevated water depth (i.e. the water depth when the broad side of the rod was facing the oncoming water-flow) at each sampled riffle, following Fonstad et al. (2005). We assessed bed stability using the stream-bed component of the Pfankuch stability index (Death & Winterbourn, 1994; Pfankuch, 1975). We scored rock angularity, brightness, consolidation, substrate size distribution, percentage stable materials, scouring and clinging vegetation based on predetermined quantitative categories. The index sums the score given to each characteristic. Lower total scores indicate more stable stream bed. We assessed substrate size composition by measuring the beta axis of 100 randomly selected stones using the Wolman Walk method (Wolman, 1954) and grouping them into Wentworth scale size classes (Cummins, 1962; Wentworth, 1922). We calculated the substrate size index (SI) by summing the midpoint values of each class weighed by their proportion (Quinn & Hickey, 1990b). Bedrock was assigned the 400 mm value (Tonkin, 2014). Stream segment slope was acquired from the FENZ database. Conductivity and water temperature were spot-measured using an Oakton ECTestr 11 dual-range pocket meter. Percentage of undercut banks, debris jams and riparian land cover (native forest, native shrub, planted forest, pasture, bare ground) at a radius of 25 to 50 m around the sampling reach were visually assessed. Finally, we scored the embeddedness of the substrate (1=loose, 2=moderate, 3=good, 4=tight) (Death

& Joy, 2004). For the analysis of the adult assemblages, we additionally measured air temperature during light trapping with a Hobo Pendant Temperature Data Logger UA-002-64. The percentage of the stream area forming pools, runs, riffles and rapids was also visually assessed, as well as the abundance of protruding rocks on a qualitative scale (0=none, 1=rare, 2=moderately abundant, 3=abundant).

Table 4.1: Summary statistics of habitat variables measured from 15 streams* in the Tongariro National Park, Aotearoa New Zealand, March 2017.

	Min	Max	Mean	SE
Depth (m)	0.10	0.22	0.17	0.01
Velocity (m / s)	0.52	0.94	0.76	0.03
% CPOM	0	8	2.1	0.54
Segment slope	0.55	2.86	1.34	0.20
Water Temperature (°C)	8.7	14.5	11.5	0.45
Conduct (µS / cm)	40	250	95.3	13.52
% algal filament cover	0	50	13.0	4.47
% algal mat cover	0	70	17.8	4.92
% algal film cover	25	93	51.2	4.98
% periphyton-free substrate	5	35	18.0	2.38
Embeddedness	0	3	1.5	0.26
Pfankuch Index	25	53	34.0	1.72
Substrate Index	48.1	165.3	100.1	7.26
Chlorophyll α (µg /cm2)	0.24	5.53	2.97	0.45
Altitude (m)	520	1176	777.5	41.09
Width (m)	3.8	13.1	6.9	0.71
% canopy cover	0	77	27.1	7.31
% native forest	0	50	22.3	4.19
% native shrub	30	80	52.7	3.16
% exotic forest	0	40	7.3	3.96
% bare ground	5	30	17.7	2.38
% undercut banks	10	80	55.7	4.36
% debris jams	0	10	2.2	0.77
Moss	1	2	1.5	0.13
Macrophytes	0	2	0.9	0.18
% pool area	0	40	8.3	3.22
% run area	5	80	39.9	5.93
% riffle area	15	92	44.2	5.22
% rapid area	0	55	7.3	4.33
Protruding rocks	1	3	2.6	0.16
Air Temperature (°C)	9.1	13.9	11.7	0.44

* Site nr.2, Waitaiki Stream, downstream from Lake Rotokuru, was excluded from the initial 16 streams

4.2.6 Data analysis

Analyses were performed with the R software v.3.5.1 (R Core Team, 2020). Waitaiki Stream (site 2) was just downstream from Lake Rotokuru and both its macroinvertebrate community and environmental variables were substantially different from the rest of the streams. It was thus excluded from the final analysis. To compare benthic and flying assemblages, we also analysed the benthic caddisfly assemblages separately from the other benthic fauna. We standardized the environmental data to a mean of zero and variance of one.

We examined whether macroinvertebrate communities or environmental conditions were spatially autocorrelated, by performing a Mantel test based on Pearson's product-moment correlation with 999 permutations, with the *mantel* function in the Vegan package (Oksanen et al., 2018). We compared distance matrices of the spatial locations (New Zealand Transverse Mercator coordinates) with dissimilarity matrices of the environmental variables and assemblages, using the *vegdist* function in the same package. We used Euclidean distances for coordinates and environmental variables and Bray-Curtis distances for log(x+1) transformed macroinvertebrate data. Waterway distances were not used, as not all streams belonged to the same catchment.

To examine redundancy among correlating environmental variables, we performed Spearman's rank correlations among the standardized environmental variables with the *rcorr* function of the Hmisc package (Harrell Jr & Dupont, 2019). P-values were adjusted using the method of (Benjamini & Hochberg, 1995). No significant correlations were found for any pair of environmental variables and so all were retained for analysis (Appendix C: Table S4.1).

To summarize the environmental data and visualize existing gradients among our sites, we performed principal component analysis (PCA) with the Vegan package. The

number of principal components (PCs) to be retained was evaluated using the Broken-stick model (Jackson, 1993). PCs' eigenvalues were compared to values in a broken-stick distribution and the components with eigenvalues higher than their broken-stick equivalents were retained.

We calculated effective species richness (the exponential of the Shannon diversity index, hereby called diversity) and relative taxonomic evenness (Pielou's J index, hereby called evenness) for the total communities and the common and rare assemblages in each stream. We explored the environmental drivers of these metrics with Partial Least Square Regression (PLSR) and leave-one-out-cross-validation (LOOCV) with the *plsr* function of the pls package (Mevik et al., 2019a). This analysis is suitable for potentially intercorrelated predictor variables, with sample sizes that are small compared to the number of predictors (Carrascal et al., 2009). It decomposes the dependent and explanatory variables in latent structures consisting of a number of components, so that the maximum variation in the dependent variable is explained by the loading of the explanatory variable projected on the components of its corresponding latent structure. We focused on the first components of the latent structures, which explained in general higher percentages of variation. We determined the variables that were important in predicting the biodiversity metrics with the Variable Importance in Projection (VIP) approach and calculated the VIP score with the VIP function (Mevik et al., 2019b). The VIP score is a weighted sum of squares of the PLS loadings on the components of the latent structures, which takes into account the explained variance of the PLS component. We selected variables with VIP > 1, as the average squared VIP scores are close to 1 (Chong & Jun, 2005), and considered as drivers, variables with strong and moderately strong loadings, > 0.25 or < -0.25, as the strongest loadings were |0.6|.

To determine the subset of environmental variables that correlated best with community structure, we performed BioEnv (Clarke & Ainsworth, 1993) on log(x+1) transformed abundance data, with the function *bioenv* in the Vegan package. Euclidean distances for the standardized environmental variables were rank correlated with community Bray-Curtis dissimilarities. The best subset of environmental variables had the highest Spearman rank correlation with the community dissimilarities. We assessed the significance of these correlations with a Mantel test between the environmental distances (function *bioenvdist* in the vegan package) and the community dissimilarities, with 9999 permutations. We tested the concordance between the assemblages' NMDS ordinations (Bray-Curtis distances in two dimensions) and the environmental variables' PCA ordination with the Procrustes analysis in the vegan package and its significance with the Procrustes randomization test (function *protest*). To limit statistical noise, we ran this analysis for all environmental variables and the subsets identified by BioEnv correlating most with each assemblage's dissimilarities matrix.

4.3 Results

The 15 second to fourth order reaches sampled ranged in width between 3.8 and 13.0 m (mean = 6.9 m), and their conductivity ranged between 40 and 250 μS/cm (mean = 95 μS/cm) (Table 4.1). There was no evidence of the habitat variables being spatially correlated and PCA did not reveal significant gradients. Of the invertebrate data only the common component of the Surber samples were spatially correlated ($r = 0.24$, $p = 0.03$).

4.3.1 Environmental drivers of biodiversity metrics

In total 91 taxa were identified from the benthic samples (35 were caddisflies). The light traps collected 34 caddisfly species. Diversity of rare taxa was three to four times higher

($p < 0.001$) than for the common taxa for all datasets (Table 4.2). Evenness did not differ between the rare and common assemblages for the benthic samples ($p > 0.05$), but the evenness of the rare species of the light traps was more than double that for the common species ($p < 0.001$).

The variation in benthic biodiversity metrics explained by the measured environmental variables (Table 4.3) was marginally higher for the common than rare components (61 and 59%, respectively for diversity, and 65 and 62, respectively for evenness). All components of the communities exhibited similar relationships between biodiversity metrics and habitat variables (Fig. 4.2). They were positively linked with water temperature, undercut banks and exotic forest riparian cover, and negatively linked with altitude, slope, mosses and filamentous algae. Common components' biodiversity was positively related to substrate stability and embeddedness; these were also important for the total component. Rare components' biodiversity was negatively linked to native forest and positively linked to CPOM.

The difference between the biodiversity metrics' variance explained by the environmental variables was also marginal for the diversity of common and rare benthic caddisflies (53 and 52% respectively), but larger for evenness (66 and 53%, respectively). Both metrics describing the common and rare components showed largely similar relationships with the environmental variables. The total assemblages had a similar pattern but in the opposing direction to the common and rare components (Fig. 4.3); i.e. when the two components were positively related to an environmental variable, the total assemblage was negatively related to that same variable. Altitude and slope were linked negatively to both common and rare biodiversity metrics and undercut banks were linked positively. Water temperature and stream bed stability were linked positively to the common components, and mosses and filamentous algae negatively. Embeddedness was

positively linked to the rare component and the total community. Rare biodiversity was positively related to exotic forest and chlorophyll a, while substrate size and native forest had moderately negative loadings. Macrophytes were not linked to any of the two components, but they were positively linked to the total communities.

Explained variation in the adult caddisfly communities' diversity was lower for CCA than RCA (60 and 79%, respectively), while the opposite was observed for evenness (90 and 65%, respectively). Patterns were much more variable for the adult caddisfly assemblages (Fig. 4.4), with only percentage of rapids being related with all three components, positively with the common components and negatively with the rare and the total components. Diversity of both common and rare components was positively linked with stream width and negatively related to debris jams and canopy cover. The common components were also positively related to altitude, slope, velocity and native shrub coverage. The rare components were negatively linked to mosses, macrophytes and planted forest coverage, and positively related with native forest, air temperature, run percentage, undercut banks and vegetation free ground. Riffles were negatively linked to the total communities, but not equally strongly to any of their components. The same pattern for the total components, as for the benthic caddisflies, for some variables. While common and rare taxa were positively related (or tended to be positively related, with non-significant loadings) to e.g. slope and velocity, the total components were negatively related to them.

Table 4.2: Biodiversity metrics of macroinvertebrate communities and their common and rare components, sampled with Surber samplers and UV-light traps in 15 & 14 streams respectively, in Tongariro National Park, New Zealand, March 2017.

Method	Metric†	Assemblage‡	Min	Max	Mean	SE
Surber	EfNSp	TIA	4.04	16.51	10.52	0.92
		CIA	2.49	10.03	5.71	0.56
		RIA	12.83	25.82	19.80	1.05
	Rev	TIA	0.40	0.72	0.61	0.02
		CIA	0.59	0.96	0.84	0.03
		RIA	0.77	0.89	0.84	0.01
Surber Trichoptera	EfNSp	TCA	2.70	10.30	5.27	0.49
		CCA	1.00	3.70	2.22	0.23
		RCA	6.34	12.13	9.66	0.51
	Rev	TCA	0.33	0.79	0.56	0.03
		CCA	0.00	1.00	0.70	0.09
		RCA	0.70	0.95	0.83	0.02
UV-light Trichoptera	EfNSp	TCA	2.27	10.97	5.97	0.73
		CCA	1.00	4.06	1.54	0.28
		RCA	2.42	11.05	6.75	0.81
	Rev	TCA	0.35	0.96	0.76	0.05
		CCA	0.00	0.98	0.36	0.12
		RCA	0.65	0.96	0.87	0.02

† EfNSp = Effective number of species, REv = Relative evenness,
‡ TIA = Total Invertebrates Assemblage, TCA = Total Caddisflies Assemblage, CIA/CCA = Common, RIA/RCA = Rare
SE = Standard Error

Table 4.3: Partial least squares regression of diversity and evenness, from 15 Surber and 14 UV-light trap-sampled stream macroinvertebrate assemblages and their common and rare components, collected in the Tongariro National Park, New Zealand, March 2017.

			Training dataset (% variance explained)		Cross validated
	Metric†	Component‡	Env. Var§	MI§	RMSE§
Surbers	EfNSp	TIA	19	57	3.56
		CIA	16	61	2.36
		RIA	18	59	3.81
	REv	TIA	19	66	0.08
		CIA	18	65	0.1
		RIA	17	62	0.02
Surbers Trichoptera	EfNSp	TCA	17	61	1.99
		CCA	15	53	1.07
		RCA	17	52	2.27
	REv	TCA	18	59	0.12
		CCA	17	66	0.36
		RCA	17	53	0.07
UV-Light Trichoptera	EfNSp	TCA	17	66	2.69
		CCA	21	60	1.06
		RCA	19	79	2.32
	REv	TCA	14	50	0.26
		CCA	26	90	0.28
		RCA	16	65	0.09

† EfNSp = Effective number of species, REv = Relative evenness,
‡ TIA = Total Invertebrates Assemblage, TCA = Total Caddisflies Assemblage, CIA/CCA = Common, RIA/RCA = Rare
§ Env.Var = Environmental variables, MI = Macroinvertebrates, RMSE = Root Mean Square Error

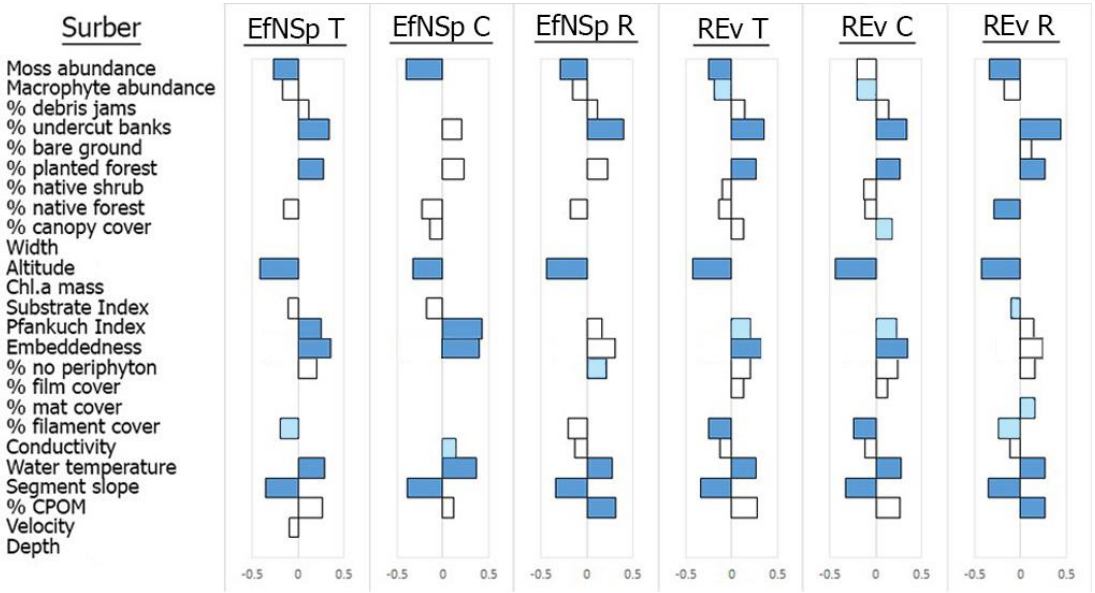

Figure 4.2: Loadings of 25 environmental variables on the first component of partial least squares regression models for effective species richness and relative evenness of benthic macroinvertebrate communities collected from 15 streams in the Tongariro National Park, New Zealand, March 2017. Coloured bars indicate Variable Importance in Projection scores > 1. Dark blue bars indicate environmental variable loadings > 0.25 or < -0.25. Light blue bars indicate loadings between -0.25 and 0.25. ● EfNSp = Effective number of species, REv = Relative evenness ● T = Total Invertebrates Assemblage, C = Common assemblage, R = Rare assemblage

4.3.2 Environmental drivers of community structure

Across all assemblages, 19 of the 25 measured habitat variables were linked with assemblage structure (Table 4.4). Altitude, water velocity, temperature, canopy cover, percentage of debris jams, substrate size, chlorophyll a and moss abundance were most strongly linked to community structure. Inclusion of rare species in benthic datasets decreased the strength of the correlation between the environment and TIA, but for the caddisfly assemblages, their inclusion strengthened the relationships. The rare component of adult caddisflies correlated more strongly with the habitat variables than the total communities, but we could not perform multivariate analyses on the adults' CCA because of limited data.

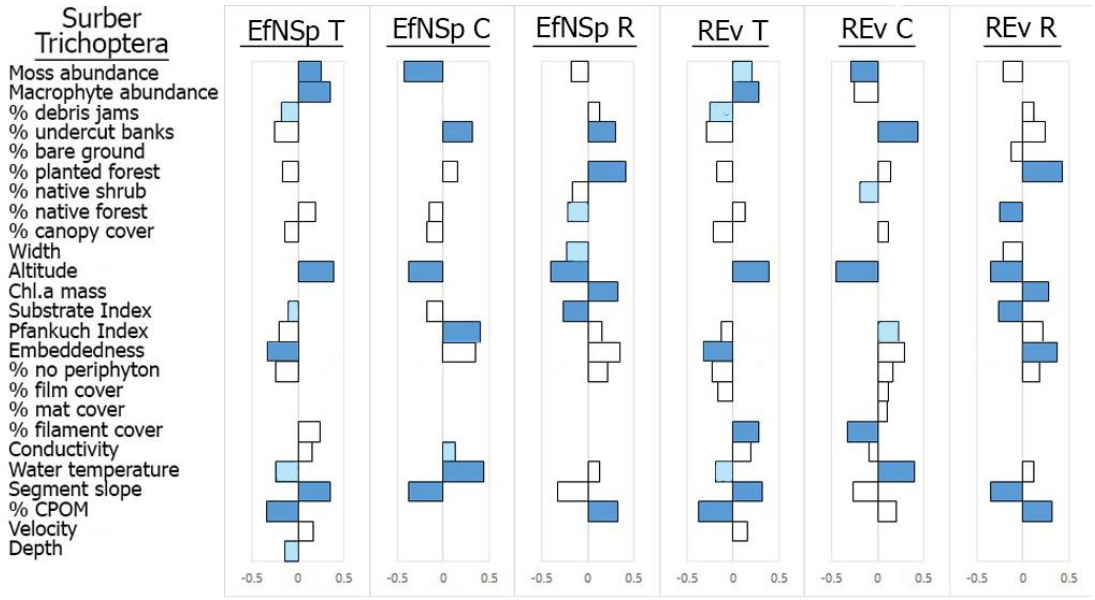

Figure 4.3: Loadings of 25 environmental variables on the first component of partial least squares regression models for effective species richness and relative evenness of benthic caddisfly communities collected from 15 streams in the Tongariro National Park, New Zealand, March 2017. Coloured bars indicate Variable Importance in Projection scores > 1. Dark blue bars indicate environmental variable loadings > 0.25 or < -0.25. Light blue bars indicate loadings between -0.25 and 0.25. ● EfNSp = Effective number of species, REv = Relative evenness ● T = Total Caddisflies Assemblage, C = Common assemblage, R = Rare assemblage

TIA (r_{TIA} = 0.54) were modelled best in BioEnv by velocity, canopy cover, altitude, chlorophyll a and native shrubs (Table 4.4), with the first three contributing most to the relationship (r = 0.44). CIA (r_{CIA} = 0.61) and RIA (r_{RIA} = 0.49) were modelled by 10 variables. Velocity, water temperature, depth, periphyton-free substrate, chlorophyll-a and mosses were important for both. The biggest contribution to the correlation with the CIA was substrate size, velocity, water temperature and native forest percentage (r = 0.55). RIA were driven mostly by velocity, exotic forest, canopy cover and altitude (r = 0.47).

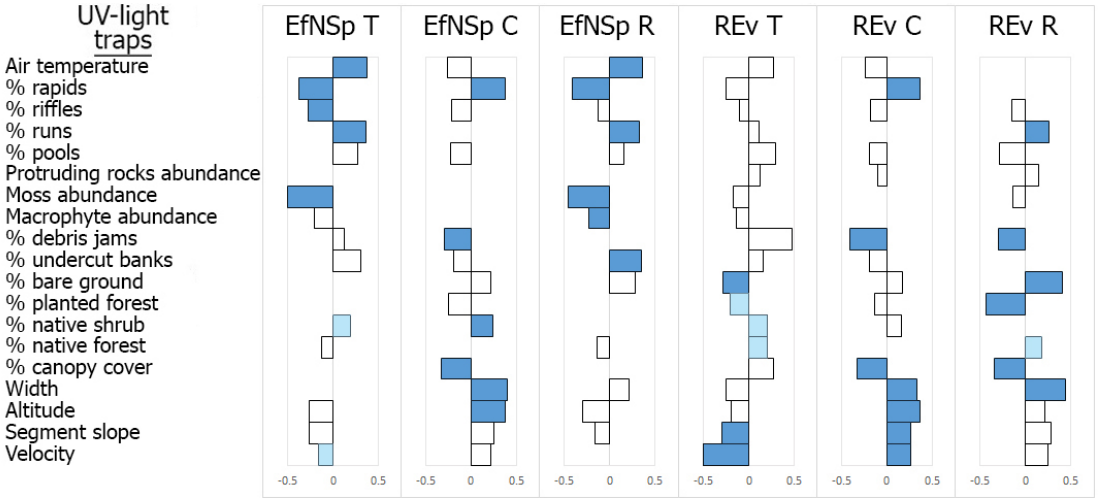

Figure 4.4: Loadings of 19 environmental variables on the first component of partial least squares regression models for effective species richness and relative evenness of adult caddisfly communities collected with UV-light traps from 14 streams in the Tongariro National Park, New Zealand, March 2017. Coloured bars indicate Variable Importance in Projection scores >1. Dark blue bars indicate environmental variable loadings > 0.25 or < -0.25. Light blue bars indicate loadings between -0.25 and 0.25. ● EfNSp = Effective number of species, REv = Relative evenness ● T = Total Caddisflies Assemblage, C = Common assemblage, R = Rare assemblage

Benthic TCA correlated with 11 habitat variables (r_{TCA} = 0.62) (Table 4.4). Altitude, chlorophyll-a and moss abundance were responsible for the biggest percentage of correlation (r = 0.5), with another four variables (filamentous algae, canopy cover, water temperature and native shrub) contributing between 0.02 and 0.03. CCA and RCA correlated best with seven and four variables respectively (r_{CCA} = 0.58 & r_{RCA} = 0.5). CCA (r_{CCA} = 0.58) were most strongly linked with chlorophyll-a (r = 0.33), while native forest riparian coverage, canopy cover, velocity, macrophytes abundance and planted forest contributed between 0.08 and 0.02. RCA were also driven by canopy cover, velocity and planted forest coverage, which contributed the most to the correlation (r_{RCA} = 0.5).

UV-light trap communities were modelled best by seven habitat variables (r_{TCA} = 0.51, Table 4.4). The largest effect on the correlation was exerted by debris jams, moss

abundance, altitude and riffle percentage (r = 0.45). The common component was overly sparse and could not be analysed. RCA had a higher correlation (r_{RCA} = 0.60), mostly because of rapids, moss abundance and native riparian shrub coverage (r = 0.54).

Table 4.4: Correlation of environmental data and community structure. BioEnv analysis indicated the subsets of environmental variables that were best correlated with community structure in Surber samples and UV-light traps from 15 and 14 streams respectively in Tongariro National Park, New Zealand, March 2017.

	TIA/TCA†		CIA/CCA†		RIA/RCA†	
	Variable	r_s	Variable	r_s	Variable	r_s
Surber	Velocity	0.24	Substrate Index	0.31	Velocity	0.28
	% canopy cover	0.35	Velocity	0.46	% planted forest	0.40
	Altitude	0.45	Water Temp	0.51	% canopy cover	0.44
	Chlorophyll-a	0.51	% native forest	0.55	Altitude	0.47
	% native shrub	**0.54**	Depth	0.57	Moss abundance	0.49
			% no periphyton	0.58	Depth	0.48
			% debris jams	0.59	% no periphyton	0.48
			% filament cover	0.60	Water Temp	0.48
			Chlorophyll a	0.61	% bare ground	0.49
			Moss abundance	**0.61**	Chlorophyll a	**0.49**
Surber Caddisflies	Altitude	0.36	Chlorophyll a	0.33	% canopy cover	0.30
	Chlorophyll a	0.47	% native forest	0.41	Velocity	0.43
	Moss abundance	0.50	% canopy cover	0.49	% planted forest	0.50
	% filament cover	0.52	Velocity	0.53	Depth	**0.50**
	% canopy cover	0.54	Macrophyte abun	0.55		
	Water Temp	0.57	% planted forest	0.57		
	% native shrub	0.60	Moss abundance	**0.58**		
	% planted forest	0.61				
	Velocity	0.62				
	% undercut banks	0.62				
	Macrophyte abun	**0.62**				
UV-light trap Caddisflies	% debris jams	0.32			% rapid	0.36
	Moss abundance	0.37			Moss abundance	0.49
	Altitude	0.42			% native shrub	0.54
	% riffle	0.46			% planted forest	0.56
	Air Temperature	0.49			Air Temperature	0.58
	% planted forest	0.50			% undercut banks	**0.60**
	Velocity	**0.51**				

† TIA = Total Invertebrates Assemblage, TCA = Total Caddisflies Assemblage, CIA/CCA = Common assemblage, RIA/RCA = Rare assemblage

4.3.3 Concordance of communities and environmental drivers

Assemblage NMDS and habitat variable PCA ordinations were only concordant for the benthic CCA (r = 0.58, p = 0.01) (Table 4.5). However, when we limited the habitat

variables to those found to be significant in the previous analysis, the other two components of the benthic caddisflies assemblages also correlated. However, the lowest correlation was found with the TCA (r = 0.5, p = 0.05), while both CCA (r = 0.61, p = 0.01) and RCA (r = 0.78, p < 0.001) correlated more strongly. PCA also correlated significantly with adult TCA ordination (r = 0.66, p = 0.003).

Table 4.5: Correlation between the ordinations of the environmental variables and of macroinvertebrate community assemblages and their common and rare components, collected with Surbers and UV-light traps from 15 and 14 streams respectively in Tongariro National Park, New Zealand, March 2017.

Method	Assemblage†	NMDS stress	Procrustes			Procrustes (BioEnv variables only)		
			SS	corr	sig	SS	corr	sig
Surber	TIA	0.11	0.82	0.43	0.14	0.77	0.48	0.06
	CIA	0.11	0.91	0.29	0.49	0.88	0.34	0.36
	RIA	0.17	0.90	0.31	0.47	0.80	0.44	0.11
Surber Caddisflies	TCA	0.10	0.79	0.46	0.09	0.75	0.50	**0.05**
	CCA	0.04	0.66	0.58	**0.01**	0.63	0.61	**0.01**
	RCA	0.15	0.84	0.41	0.20	0.40	0.78	**0.00**
UV-light trap Caddisflies	TCA	0.13	0.80	0.45	0.14	0.72	0.53	**0.04**
	RCA	0.17	0.81	0.43	0.17	0.95	0.22	0.82

† TIA = All Invertebrates Assemblage, CCA = All Caddisflies Assemblage, CIA/CCA = Common assemblage, RIA/RCA = Rare assemblage

SS = Sum of Squares; Significance level: < 0.05

4.4 Discussion

Drivers of biodiversity have been more thoroughly studied in terrestrial ecosystems compared to freshwater ones (Heino, 2002). Biodiversity patterns in lotic ecosystems vary in a different way to terrestrial ones because of the physical differences between aquatic and terrestrial habitats. Streams and rivers are strongly dependent on the downstream flow of water, water quality, connectivity and frequency and magnitude of

disturbances (Silva et al., 2016). Whether the numerous rare macroinvertebrate species are related to the same habitat characteristics and in the same way as the common species, is still unclear (Cao et al., 1998, 2001; Cao & Williams, 1999; Marchant, 1999, 2002). Adult aquatic macroinvertebrates have been suggested as a complementary assemblage to inform freshwater ecology understanding (Joy & Death, 2013), but the resemblance of the relationships between habitat characteristics and common and rare components of benthic and flying aquatic macroinvertebrate assemblages have not been extensively evaluated.

4.4.1 Relationships between benthic macroinvertebrate community structure and habitat variables

Inclusion of rare taxa in the analysis did not affect the potential of environmental characteristics to explain variation in community biodiversity metrics, opposing the argument that they increase statistical noise (Marchant, 1999, 2002). Similar sets of habitat variables were linked with the diversity of both common and rare community components, and in the same way (positively or negatively), such as the streams' physical characteristics (e.g. temperature, slope, undercut banks), altitude and vegetation (riparian and instream). While this could suggest rare species contain redundant information that is already carried by the common species (Marchant, 1999), similar patterns between common and rare species do not necessarily mean their niches are the same. They can be related to the same habitat variables (Siqueira et al., 2012), in a similar way, but with unequal strength. The loadings of the environmental variables on the latent structures describing the biodiversity metrics in the PLSR analysis, and the importance of those loadings, indicated by their VIP scores, suggested such differences in the relationships between the community components and their habitat. Rare species' inclusion had mostly

positive or negligible impacts on revealing the relationships between the communities' biodiversity metrics and the environment; only rarely did they mask them, in already weak relationships between the common taxa and their habitat. Rare taxa do not, therefore, obscure the patterns observed with common taxa, and may even facilitate explanations in deriving environmental driver and biodiversity metric relationships.

The structure of the rare components correlated weakly with the habitat variables in comparison to the common taxa. Both components correlated best with sets of both physical and resource related variables, as is common in headwater streams globally (Benson & Pearson, 2020). They shared several of those environmental variables (Table 4.4), but only velocity was significant for both. Velocity and flow have been linked more closely with abundant and widespread taxa than with rare ones (Nijboer & Schmidt-Kloiber, 2004; Sarremejane et al., 2018). In our study, velocity was more important for the structure of the rare components. In general, common taxa appeared to be related more strongly with variables that affected the whole stream reach, while rare taxa with variables characterized with a patchier distribution. The common components were linked with physical stream characteristics (substrate size, temperature and depth) and resource-related variables (native riparian forest). New Zealand streams are characterized by floods, which disturb the streambed by removing and rearranging substrate particles (Quinn & Hickey, 1990b; Winterbourn et al., 1981). Along with temperature, substrate size can have an overarching effect on the community and thus the common taxa can be expected to be strongly related to these. Rare taxa were related more to a different set of physical and resource variables (altitude, mosses, exotic riparian forest and canopy cover). Mosses can provide complex but limited patches of habitat and host rare species (Sgarbi & Melo, 2018). Streams flowing through mature pine plantations may host communities similar to those in native forest areas (Quinn et al., 1997, 2004), or clearly

differentiated, having lost local species and resources (Harding & Winterbourn, 1995). However, as they provide food resources to the stream communities that would otherwise be absent from New Zealand streams, they could host additional rare species.

The total assemblages correlated best with fewer variables than their two components did, sharing four with the rare components and only two with the common ones. Faith & Norris (1989) found more relationships with the environment when they included rare species in analyses, but they included several chemical variables, while we focused on physical instream and riparian characteristics. Chemical variables were not considered in our study, as they were not expected to differ significantly, because of the spatially limited pristine study area, without pollution gradients. However, the correlation of the total communities to the environment was weaker than that of the common components (Table 4.4). More taxa, with more diverse responses to their environment, can be expected to weaken the relationship of the total assemblage with it. Even though rare taxa were shown to be more variably related to their environment than the common ones, they carried information that was complementary, instead of redundant, to that of the common ones (Marchant, 1999; Reddin et al., 2015), thus being equally important in revealing relationships between benthic communities and the environment (Heino, 2008).

Even though marginally non-significant, the ordination of the complete communities correlated more strongly with the ordination of the selected subset of environmental variables, than did the ordinations of their components. Arscott et al. (2006) found that in better-quality streams rare taxa revealed more, and stronger relationships with the environment, while in lesser-quality streams information in rare taxa was redundant. The general absence of significant correlations between the ordinations of communities and habitat variables might be related to the natural variation of the latter (Sgarbi & Melo, 2018) and the lack of clear gradients across our relatively

small, pristine area. Records came from spot measurements, under ideal sampling conditions (normal low flows, clear water), but over the weeks preceding sampling, there had been heavy rainfalls in the central North Island (Brandolino, 2017). Disturbances such as high flows and floods could have restructured the communities (Death, 1996). Despite the uncertainty, our results suggested it is advantageous to include both common and rare components in multivariate analyses.

4.4.2 Relationships between benthic caddisfly assemblages' structure and habitat variables

Inclusion of rare benthic caddisflies facilitated the explanation of the diversity patterns with the environment but not of the evenness patterns. Both components showed the same positive or negative trends in the relationships between their biodiversity metrics and the environment, but with more variable patterns in the strengths of these relationships than the complete communities. However, inclusion of the rare taxa, despite maintaining these relationships, reversed their sign. This seems counterintuitive but could be explained through niche correlation among caddisfly species, with clearly distinguished optima and minima along the niche continuum (Vilmi et al., 2019). Caddisflies are often indicative of environmental quality (Bonada et al., 2004; Resh, 1992), but in such a small study area with no major environmental gradients, they can comprise species with similar niches. This can render species common where their requirements are satisfied and rare where small differences make the environmental conditions less than ideal. Despite the two components being similarly linked to the environmental variables, the total communities thus showed an inverse pattern. Such radically different results obtained by including and excluding rare taxa demand careful consideration when applied in freshwater studies. As the patterns of each component are similar to those of the complete communities, the

inclusion of the rare component in the analysis seems to be distorting the relationships of the caddisfly biodiversity metrics to their environment.

Inclusion of rare taxa led to the strongest correlation between the structure of any group of assemblages and their environment in the study. Apart from supporting the use of caddisfly larvae (usually along with mayflies and stoneflies) in bioassessment (Bonada et al., 2004; Resh, 1992), it also suggested complementarity of the information carried by the two components. This was not expressed through different variables correlating with each component, as the variables best correlating with the rare assemblages (canopy cover, velocity and exotic forest) were also linked to the common ones. Instead, additional variables were linked to the total assemblages, suggesting that the complete assemblages revealed more and overall stronger relationships.

Inclusion of rare taxa in multivariate ordination analysis obscured the correlation patterns between the ordination of the environmental variables and the common taxa. This pattern was partially reversed when the analysis was limited to the BioEnv-indicated variables, with the rare component correlating more strongly with their set of habitat variables than the other components. The incongruence between the correlation of common and rare components with their environment might also be a result of their ecological niches. The correlation of the rare components with only four variables might stem from them being strict in their minimum requirements for a limited number of factors. At the same time, they could reach higher abundances, and belong in the common component, under a wider range of environmental conditions. This flexibility in requirements can be responsible for the lower correlation of the common components, rendering the common component “noisy” instead (Arscott et al., 2006; Cao, Bark, et al., 1997).

4.4.3 Relationships between adult caddisfly assemblages' structure and habitat variables

Environmental variables explained higher percentages of variation in adult caddisfly diversity when the rare species were included and in evenness when they were excluded. However, the latter seems unlikely to be anything more than coincidence. The common component of the dataset was sparse and variable because of the sample timing in early autumn, characterized by low overnight temperatures and often rain, which can have a strong negative effect on insect flying activity (Southwood & Henderson, 2000). Biodiversity metrics were more variably related with the environment than those of the benthic caddisflies. In general, rare components were suggested to drive the relationship of the total communities' diversity to the environment, while the common components were often showing contrasting trends. These could partly be a product of the common component's sparse data matrix and the rarity definition we employed. On the other hand, the relationship of evenness with the environment was similar for the two components, but their combination revealed the opposite pattern, similar to the patterns seen for the benthic caddisflies. In general, the higher variability of the trap samples could possibly be a combined result of timing, weather and the particular characteristics of UV-light traps. These factors need to be taken into account when considering the use of UV-light trap samples in freshwater studies; they selectively collect polarotactic species that are attracted by the particular UV-wavelength emitted by each trap design (Horvath & Kriska, 2008). Additionally, their effect cannot be easily limited only to the insects of a specific stream, and individuals might be attracted even from non-lotic waterbodies such as lakes, springs and seepages (Gerecke et al., 2007). Snapshot trap samples can also be heavily affected by the local weather conditions (Collier & Smith, 1998). Consequently, traps can

be susceptible to collecting “noisy” samples, potentially representative of a specific component of the community, irrespectively of the rarity status of their species.

The rare components correlated better with the environmental variables than did their combination with the common components, also probably because of the sparse and variable nature of the common components of these samples. The rare components were mostly related to rapid habitats, which, albeit not occurring so frequently, were a dominant element in the sites they were recorded in high percentages. They can affect the caddisflies and their perception of their environment, as light is not polarised on the rough surface of the water in rapids and the insects are not attracted to it. Relationships with the total component were more mixed, but debris jams were the most related and relevant variable. Debris jams and mosses cover a small percentage of the sampled habitats, but can host high densities of mayflies, stoneflies and caddisflies and even rare species (Baillie et al., 2019), and they can also offer relatively stable oviposition sites for adult individuals. Even though air temperature was not shown to have a dominant effect on community structure, it was nevertheless among the variables that were related with the structure of both rare and total components, while the activity of the caddisflies can also be affected by the temperatures over the nights previous to the sampling occasion.

The ordination of the total assemblages had stronger linkages with the environmental variable ordination than the rare components, whose ordinations did not. In part this may stem from the relatively small number of trapped individuals, which rendered both common and rare components necessary for describing the dissimilarities between communities across ordination space, while also describing the relationships with the dissimilarities of the environmental variables. It may also relate to the use of habitat variables focused on the larvae in the analysis; some species may be common as larvae but rare as adults. Light-trapping is logistically more inclined to generate a “rare”

sample of the available fauna because adults have periodic flight timing and pattern and are variably attracted to UV-light. Thus, rare species collected as adults may actually relate more to common larvae whose abundance is strongly linked with the environment. Thus, when dealing with a data assemblage that is a small temporal snapshot of the prevailing fauna it is of benefit to include all species.

4.4.4 Implications for rare taxa inclusion in the discovery of relationships between macroinvertebrate communities and environmental habitat

The present study suggests that the habitat characteristics most strongly linked with aquatic macroinvertebrate assemblages can vary between total, common and rare components of the communities depending on the taxonomic group, life stage and the particular metric or statistical method used. Being rare at a certain point in time and space might indicate adverse or simply non-ideal conditions, contrasting the response of the same species under favourable conditions or other species that are common in the same sample (Sgarbi & Melo, 2018). Sampling method (Nijboer & Schmidt-Kloiber, 2004), rarity definition (Cucherousset et al., 2008) and stochastic events might also affect the structure of the rare components (Bunn & Hughes, 1997). Defining rarity based on species abundance in each site separately will have a different effect on the structure of the common and rare components in comparison to rarity definitions based on abundance or site occupancy over the whole study area (Chapter 2). A site-specific definition will create different common and rare components in each site, while an "over the whole study" definition will separate them uniformly. The latter-type definitions also avoid zero-inflated datasets, which are considered one of the problems of having many rare species (Barry & Welsh, 2002; Welsh et al., 1996), but will possibly miss finer differences between environmental conditions that determine the species' rarity status, especially in

small and pristine areas. Focusing on specific taxonomic groups or even species might give greater insight into the environmental factors that are related to rarity (Mandelik et al., 2010; Vermeij & Grosberg, 2018). This might then help describe more general patterns of rarity and its role in the natural world.

In summary, rare taxa were found to carry significant amounts of information, that was not just a fuzzier copy, or a subset of the information carried by the common taxa. Their inclusion often added complementary information, revealing additional relationships with the environment or supporting relationships that were seen or even only suggested by the common components.

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Chapter 5

The effect of the local environment and dispersal processes on structuring common and rare lotic macroinvertebrate assemblages along the river network.

Abstract

Macroinvertebrate communities in lotic networks are structured by local environmental (biotic and abiotic), dispersal and stochastic processes. Rare species comprise a large component of community richness and their populations can be threatened by environmental change more than common species' populations. However, they are often excluded from analyses as "noisy" data, thus not contributing the information they carry and not being accounted for in catchment management decisions. We studied the effect of stream network position and dispersal mode on common and rare benthic macroinvertebrate assemblages, in three catchments in the central North Island of Aotearoa New Zealand. Rare taxa assemblages did not differ between headwaters and mainstem streams and were not structured by either the local environment or dispersal processes. Their inclusion, however, did not mask patterns in common species assemblages and in some cases even amplified them. The small study area and its dense stream network allowed weak dispersers to closely track suitable environmental conditions, while strong dispersers had much higher dispersal potential, masking their relationship to the environment. Contrary to expectations, mainstem streams were not more species rich and diverse than headwaters. Flooding events are common in New Zealand streams and might have an overriding effect on mainstem communities. Headwater communities comprised a uniform group because of the streams' habitat similarities and dense lotic network within the small, protected area, contrasting the fewer and affected by differing land-use types, mainstem communities. Community structure was clearly differentiated between the two network positions and driven more by the local environment than dispersal processes. Inclusion of rare species did not hinder analyses in a metacommunity context but provided greater certainty instead. Conservation planning

for rare stream macroinvertebrate biodiversity requires consideration of the whole catchment, including both headwaters and mainstem reaches.

5.1 Introduction

Lotic communities are structured by a range of interacting factors related to the local and regional environment (biotic and abiotic), the species' dispersal abilities as larvae and adults, and even stochastic processes (Astorga et al., 2014; Didham et al., 2012; Grönroos et al., 2013; Sarremejane, Mykrä, et al., 2017; Tonkin & Death, 2013). Lotic ecosystem networks are distinctive because of their hierarchical dendritic architecture (Swan & Brown, 2011). More complex branching networks can host communities with higher β-diversity than simpler, less branched ones (Muneepeerakul et al., 2008). Along with the environmental conditions distinguishing aquatic and terrestrial ecosystems, this influences the spatial configuration of biodiversity patterns (Altermatt et al., 2013; Tonkin, Heino, et al., 2018).

Local environmental conditions are often found to dominate metacommunity structure ("the power of species sorting" - Grönroos et al., 2013; Gucht et al., 2007). However, Tonkin, Death, et al. (2018) found that "snapshot" sampling, especially in highly dynamic systems like streams in New Zealand, may be misleading and that the relative importance of species sorting and dispersal is context dependent. The relative contribution of species sorting and dispersal to community structure may shift along the river network ("Network Position Hypothesis" - Brown et al., 2011; Henriques-Silva et al., 2019). Headwater streams are more heterogeneous and isolated within the network than the mainstem reaches, with more variable but less diverse communities (Altermatt et al., 2013; Anderson & Hayes, 2018; Carrara et al., 2012). These communities are characterised more by dispersal limitation and species sorting, while mainstem communities are characterised by more equal combinations of species sorting and dispersal (Brown & Swan, 2010; Henriques-Silva et al., 2019; Schmera et al., 2018).

Species' dispersal rates affect their distribution across the landscape. Moderate rates allow species to reach all sites in a network and local conditions determine their establishment (Heino et al., 2015; Siegloch et al., 2018). Low rates limit species to the sites where they occur, and high rates allow them to reappear in unsuitable sites (Kärnä et al., 2015; Sarremejane, Mykrä, et al., 2017; Winegardner et al., 2012). Dispersal is approximated via e.g. habitat connectivity measures (Jacobson & Peres-Neto, 2010) and species traits (body size, dispersal mode and dispersal ability – Bie et al., 2012; Grönroos et al., 2013; Kärnä et al., 2015). Active dispersers walk, fly or swim, while passive dispersers rely on wind, water or other organisms (Bilton et al., 2001). Benthic invertebrates move in all directions, but downstream drift is considered the main dispersal mechanism (Connolly & Pearson, 2018). Flying adults are more likely to disperse long distances (Brooks et al., 2017), introduce their species into new ecosystems, particularly upstream (Elliott, 2003; Winterbourn & Crowe, 2001), or re-introduce the species into restored ones (Graham et al., 2017). Dispersal limitation is therefore potentially stronger for fully aquatic invertebrates and weaker for actively dispersing flying species (Bie et al., 2012; Bunn & Hughes, 1997), which can track suitable environmental conditions better (Altermatt et al., 2011; Valente-Neto et al., 2018).

Just like any other biological community, stream assemblages comprise a few common species and many rare ones (Cao et al., 2001; McGill et al., 2007). Species can be common in some areas and rare in others, with their populations acting as sources and sinks respectively (McCreadie & Adler, 2008). If they are rare both locally and regionally, they can be at greater extinction risk, although this is difficult to confirm for benthic invertebrates (Cao et al., 2001; Gaston, 1998). Rare species are often considered containing redundant or even noisy information, masking natural patterns in analyses (Cao et al., 1998; Roden et al., 2018).

Rarity is often considered a “trait” of weak dispersers, which are unable to find suitable habitats to reproduce (Gaston & Kunin, 1997; Resh et al., 2005). Dispersal limitation and directionality can lead to higher extinction rates of rare species (Li et al., 2019; Muneepeerakul et al., 2008). While common species can also go extinct locally, they might nevertheless persevere regionally (Altermatt et al., 2011). However, McCreadie & Adler (2019) in their study on Simuliidae did not find any strong effect of dispersal on rarity. Swan & Brown (2014) related regional rarity to habitat specialisation. They postulated that rare community components are driven by local environmental conditions and common ones by dispersal. However, Siqueira et al. (2012) did not find differences between common and rare species’ specialisation to their environment.

Despite recent intense interest in the role of dispersal and metacommunities in explaining macroinvertebrate community structure, studies on the role of dispersal for rare invertebrates remain scarce (Heino & Soininen, 2010). It is unclear whether the rare and common macroinvertebrate community components of isolated or well-connected streams differ. For this study we evaluated the diversity patterns and potential drivers (local habitat versus dispersal) for the benthic macroinvertebrate communities in three drainage basins. We hypothesised that: H1) biodiversity in mainstems will be higher than in headwaters for both common and rare community components; H2) local environmental conditions will have stronger effects on community structure than will distances between streams, as a proxy for dispersal limitation; H3) species sorting will be stronger for the rare than common component; and H4) species sorting will be stronger for the actively dispersing flying insects than for the passively dispersing ones.

5.2 Materials & Methods

5.2.1 Study area

Three of the four main river catchments originating in and draining the Tongariro National Park in the central North Island of New Zealand were sampled: the catchment of Mangawhero River (which is the main tributary of Whangaehu River) which drains the Southern side of the National Park, the catchment of Whanganui River, which drains the North-Western side of the National Park and the catchment of Tongariro River, which drains the North-Eastern side of the National Park. In each catchment we sampled three headwater streams and a corresponding site on the mainstem; the latter was located at least 34 km downstream as the crow flies from the nearest headwater sampling site (Table 5.1 and Fig. 5.1).

Table 5.1: Streams sampled for benthic macroinvertebrates in February 2018 in and around Tongariro National park, New Zealand, with respective drainage basin, network position, order, width and altitude. Easting and Northing coordinates given in the New Zealand Transverse Mercator 2000 projection

Nr.	Stream	Easting	Northing	Basin †	Network position ‡	Order	Width (m)	Altitude (m)
1	Mangawhero River	1799260	5601055	M	MS	5	9	100
2	Mangateitei Stream	1810411	5633938	M	HW	2	4.4	648
3	Mangawhero Stream	1809468	5636979	M	HW	4	6.8	675
4	Makotuku Stream	1804980	5642115	M	HW	3	6	751
5	Whanganui River	1796156	5693117	W	MS	6	28	160
6	Whakapapaiti Stream	1813558	5660869	W	HW	4	11.9	866
7	Mangatepopo Stream	1821754	5672559	W	HW	3	8	754
8	Whanganui Stream	1825174	5677994	W	HW	3	5.2	607
9	Tongariro River	1843710	5676385	T	MS	6	13.4	405
10	Waihaha Stream	1842990	5659309	T	HW	1	7.8	721
11	Oturere Stream	1837257	5659260	T	HW	4	8.2	816
12	Mangatoetoenui Stream	1835716	5653611	T	HW	4	5	978

† M = Mangawhero, W = Whanganui, T = Tongariro

‡ MS = mainstem, HW = headwater

The Park is dominated by two andesitic volcanic massifs. Its three mountains (Ruapehu, Ngāuruhoe and Tongariro) cast a rain-shadow on its east and south-east sides resulting in considerable bare ground. Vegetation varies from broadleaf & mixed beech-podocarp, to exotic *Pinus radiata* plantations, native tussock & shrubland. Outside the park, upstream from the mainstem sites land-use includes low intensity sheep and beef agriculture, and rural or semi-urban settlements (Tonkin et al., 2013).

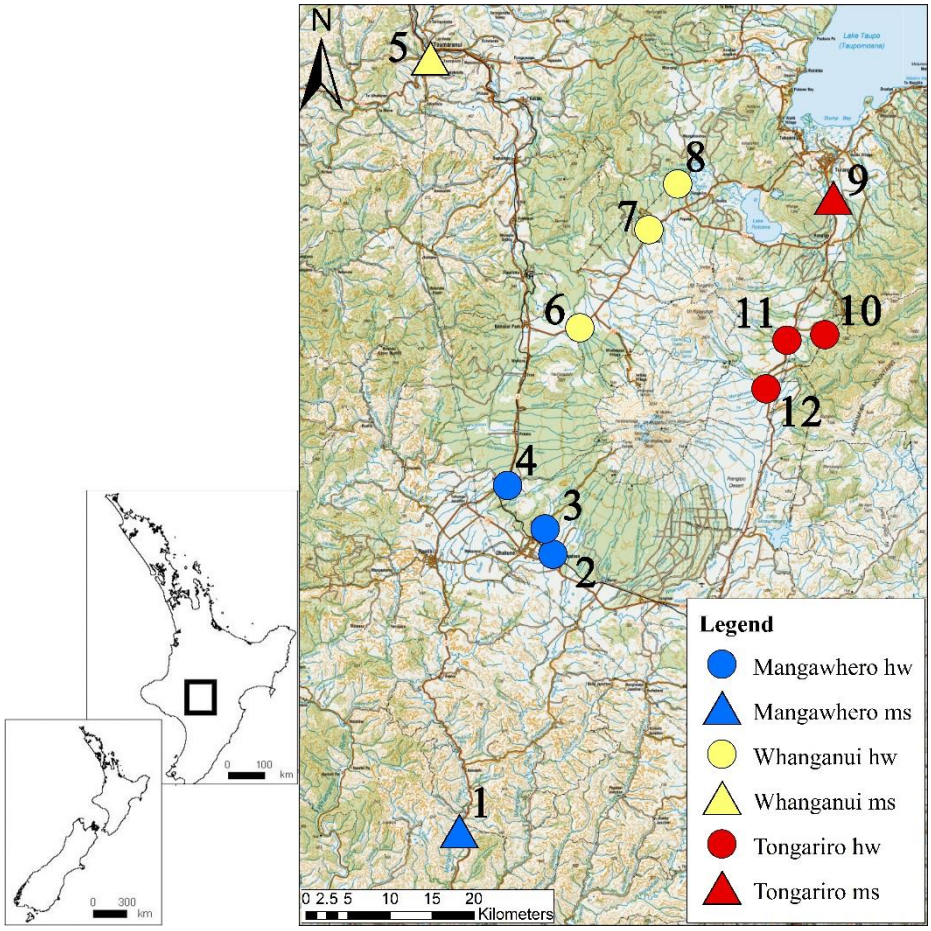

Figure 5.1: Benthic macroinvertebrate sampling locations in and around the Tongariro National Park, New Zealand, February 2018. The Mangawhero, Whanganui and Tongariro River basins were sampled, surrounding the Park, with three headwater streams (hw) and one mainstem site (MS) sampled in each basin. Numbers correspond to Table 5.1.

5.2.2 Benthic macroinvertebrates' sampling

Benthic sampling was conducted on one occasion, in February 2018, towards the end of the Austral summer. Five 0.1 m^2 Surber samples (250 μm mesh) were collected in rifle habitats, haphazardly selected within a 25-50 m reach in each stream. Samples were preserved in the field in 70% ethanol and sieved through a 500 μm mesh in the lab and enumerated invertebrates identified to the lowest feasible taxonomic level using available taxonomic keys (McLellan, 1999; Smith & Ward, 2005; Towns & Peters, 1996; Winterbourn et al., 2006). Where identification to a lower taxonomic level was not possible, individuals were classified into morphospecies based on habitus characteristics.

5.2.3 Aquatic flora measurement

The amount of chlorophyll α was measured as a proxy of periphyton biomass. Five stones from riffles in each stream were haphazardly collected (mean area = 55 cm^2) and were kept on ice, in the dark while in the field, until processed in the lab. They were immersed in 90% acetone and left in the dark, at 5 ºC, for 24 h. Absorbances were read at 664, 665 and 750 nm on a Varian Cary 50 conc UV-Visible Spectrophotometer (Varian Australia Pty Ltd, Mulgrave, Australia) and were then converted to pigment concentration following (Steinman et al., 2007). Stone surface area was estimated following (Graham et al., 1988) and halved, to take into account that only the upper half of the stone surface is available for periphyton growth.

The percentage cover of periphyton was also visually assessed within the sampling reach, as it has been shown to be a useful method for describing periphyton structure (Kilroy et al., 2013; Tonkin et al., 2014). It was characterised based on four categories; bare (no periphyton cover), thin films (0-1 mm), mats (>1 mm), and

filamentous algae. Percentage of bryophyte and macrophyte cover was also assessed on a qualitative scale (1=none, 2=rare, 3=moderately abundant, 4=abundant).

5.2.4 Physiochemical measurements

Abiotic environmental variables were measured at the same time as the benthic sampling (Table 5.2). At each sampled riffle, width and depth of the stream channel, water velocity and percentage of canopy cover were measured. Canopy cover was assessed with a spherical convex densiometer (Forestry Suppliers, Inc.); we multiplied the number of squares on its surface (max = 24) that were reflecting vegetation by 4.17 to yield the percentage canopy cover. Water velocity was estimated with a velocity head rod, by measuring water depth and the super-elevated water depth (i.e. the water depth when the rod was positioned with its broad side facing upstream) at each sampled riffle (Fonstad et al., 2005). The substrate component of the Pfankuch stability index was used to assess bed stability (Death & Winterbourn, 1994; Pfankuch, 1975). A score was assigned to each of rock angularity, brightness, consolidation, substrate size distribution and percentage of stable materials, scouring, and clinging vegetation, based on predetermined scales. The sum of these scores gives the index value. The lower the index, the more stable the stream bed. To assess the size composition of the substrate, the beta axis of 100 stones was measured. Stones were selected at random along a Wolman Walk (Wolman, 1954), and clustered into Wentworth scale size classes (Cummins, 1962; Wentworth, 1922). The percentage of particles in each class were multiplied with the midpoint of the class and summed to give the substrate size index - SI (Quinn & Hickey, 1990b). Bedrock was assigned a nominal 400 mm (Tonkin et al., 2013). Conductivity and water temperature were measured once, with an Oakton ECTestr 11 dual-range pocket meter. Mean annual stream segment flow and slope were extracted from the Freshwater Ecosystems of New

Zealand database (FENZ – Leathwick et al., 2010). Segment flow was derived from hydrological models provided by NIWA and segment slope was derived through the use of segment length and the difference between the upstream and downstream elevation of each segment (Leathwich et al., 2010). The percentages of undercut banks and riparian land cover (native forest, native shrub, planted forest, pasture, bare ground) were visually assessed. Finally, embeddedness of the stream bed was evaluated and scored on a qualitative scale (1=loose, 2=moderate, 3=good, 4=tight) (Death & Joy, 2004).

Table 5.2: Habitat variables measured from three headwater streams (HW) and one mainstem site (MS) from each of three drainage basins in the Tongariro National Park, Aotearoa New Zealand, February 2018. z values and significance levels provided from comparisons between headwater and mainstem ecosystems using Generalised Linear Mixed Models, with Gaussian distribution, network position as fixed effect and basin as random factor.

	HW				MS				
	Min	Max	Mean	SE	Min	Max	Mean	SE	z
Altitude (m)	607	978	757.3	38.5	100	405	222	93.3	**-8.27*** **
Width (m)	4.4	11.9	7.0	0.8	9	28	16.8	5.7	**3.65*** **
Depth (cm)	13	20	16.7	0.7	21	24	23	0.9	**5.50*** **
Surface Velocity (m/s)	0.8	1.1	0.9	0.03	0.8	0.9	0.9	0.04	-1.06
Flow (m^3/sec)	0.5	3.4	1.6	0.3	16	49.4	36.4	10.3	**7.42*** **
Slope (degrees)	0.6	3.4	1.2	0.3	0	1.2	0.8	0.4	-0.95
% canopy cover	8	86	47.2	9.3	5	9	6.7	1.2	**-2.93** *
% native forest	5	90	49.9	10.3	15	60	36.7	13.0	-0.74
% native shrub	0	80	38.2	8.5	10	35	25	7.6	-0.92
% bare ground	2	10	6.3	1.0	10	30	18.3	6.0	**3.70*** **
% undercut banks	0	80	57.8	8.3	10	30	18.3	6.0	**-2.84** *
Water Temperature (°C)	10.7	16.6	13.5	0.6	12.4	20.3	16.3	2.3	**2.18**
Conductivity (µS / cm)	50	240	92.2	19.7	100	160	120	20	0.83
% algal filament cover	0	2	0.4	0.3	0	20	8.3	6.0	**2.75** *
% algal mat cover	0	50	14.8	5.6	20	70	51.7	15.9	**4.34*** **
% algal film cover	30	70	52.8	5.1	15	60	31.7	14.2	**-1.98**
% periphyton-free substrate	8	65	30.9	6.3	0	15	8.3	4.4	**-3.42*** **
Moss	2	4	2.8	0.3	1	2	1.7	0.3	**-2.32**
Embeddedness	1	4	2.7	0.3	2	4	3	0.6	0.71
Pfankuch Index	23	42	33.3	2.1	26	44	36.3	5.4	0.75
Substrate Index	49	149	107	10.5	48	138	89.9	26.4	-0.79
Chlorophyll α (µg/cm^2)	0.04	0.4	0.2	0.1	0.2	1.1	0.5	0.3	**2.69** *

Significance levels: < 0.05*, < 0.01**, < 0.001***

5.2.5 Rarity definition

There is no universal definition of rarity that will apply to all species in all circumstances (Chapter 1). In the present study, taxa were considered to be rare if their abundance was equal to or less than 0.5% of the total abundance at each site, or (for samples with less than 200 individuals) equal to or less than 5 individuals. This is a commonly applied protocol in freshwater ecology to discard potentially "noisy" species data that can complicate interpretation (Sgarbi & Melo, 2018; Yu et al., 2017). The abundance of each taxon was averaged over the five Surber samples at each site and, based on these averages, taxa were defined as common or rare.

5.2.6 Dispersal groups

Macroinvertebrates were distributed into dispersal groups based on their mode of dispersal and size (Grönroos et al., 2013), using the New Zealand Freshwater Macroinvertebrate Trait Database (Phillips & Smith, 2018). Taxa without the ability to fly are limited within the stream ecosystems during all their life stages and rely mainly on downstream waterborne dispersal via drift, or less often on animal vectors. These were the non-insect benthic macroinvertebrates, passive dispersers with aquatic adults (PaAq – Appendix D: Table S5.1); Acari, Amphipoda, Collembola, Isopoda, Mollusca, Oligochaetea and Platyhelminthes. The PaAq taxa only occurred rarely; consequently, biodiversity analyses were focused on the insect assemblages (Kärnä et al., 2015).

Insects were differentiated between large, greater than 10 mm, and small, less than 10 mm. Smaller sized insects are considered weaker flyers and more easily affected by winds (Grönroos et al., 2013; Rundle et al., 2007), i.e. passive dispersers with terrestrial adults (PaTe – Appendix D: Table S5.1). These were small species of the Leptophlebiidae and Gripopterygidae families of mayflies and stoneflies, the caddisfly families Calocidae,

Conoesucidae, Helicophidae, Helicopsychidae and Hydroptilidae, most of the beetle families with the exception of Ptilodactylidae and Staphylinidae, and most of the true fly families, except for Muscidae, Tabanidae, Tanyderidae, Tipulidae and the Chironomidae genus Chironomus. The aforementioned exceptions, along with the rest of mayflies, caddisflies and stoneflies, were considered stronger flyers (Heino, 2013; Rundle et al., 2007), i.e. active dispersers with terrestrial adults (AcTe – Appendix D: Table S5.1).

5.2.7 Data analysis

Analyses were performed with the R software v.3.5.1 (R Core Team, 2020).

Habitat variables were compared between headwaters and mainstems with generalised linear mixed models (GLMMs) with Gaussian error distribution, network position as fixed effect and drainage basin as random factor. Habitat data were standardised to a mean of zero and unit variance. Habitat variables were tested for correlation, using the *rcorr* function of the *Hmisc* package (Harrell Jr & Dupont, 2019), adjusting the p-values for type I error (Benjamini & Hochberg, 1995). No significant correlations were found and thus all variables were kept in the analyses.

Principal component analysis (PCA) was performed to summarise the habitat data and indicate potential gradients among the sampled sites. The Broken-stick model (Jackson, 1993) was used to determine the number of principal components (PCs) that were most important for the ordination. PCs with higher percentages of explained variance than their equivalents of the broken-stick distribution were retained.

Univariate metrics were calculated to describe different aspects of the communities' biodiversity; species richness and abundance, which are expected to differ along the river network, but also the independent components of biodiversity, effective species richness (as the exponential of the Shannon diversity index, hereby referred to as diversity) and relative evenness (as described by Pielou's J, hereby referred to as evenness

– Jost, 2010). The metrics were calculated with the package *vegan* (Oksanen et al., 2018) for the two dispersal groups in the common, rare and total components, in the two network positions, except for relative evenness, which describes the relationship between common and rare taxa and was thus calculated only for the total communities. We also rarefied richness based on the lowest abundance of macroinvertebrates collected in any site; that was 144 individuals from Waihaha stream, the tributary of the Tongariro River. Differences between the metrics were evaluated using GLMMs with network position as fixed effect and drainage basin as random factor. Poisson error distribution was used to compare count data (species richness and abundance) and Gaussian error distribution for diversity and evenness.

Beta-diversity was assessed with the *betadisper* function of the *vegan* package on Bray-Curtis distances, which implements the PERMDISP2 procedure by Anderson et al. (2006). This procedure analyses the multivariate homogeneity of group variances and calculates the average distance to the centroid. Beta-diversity was also partitioned into its components, species replacement and species richness difference (Legendre, 2014), with the function *beta.div.comp* in the package adespatial (Dray et al., 2020). The PERMDISP2 procedure was also implemented on each component separately. A sqrt(n/(n−1)) correction controlled for the small and uneven samples (Stier et al., 2013). The statistical significance of the difference between each network position's beta diversity or any of its components was assessed with the *permutest* function and 999 permutations.

Taxonomic structure was analysed with the vegan package, using log(x+1) transformed abundance data. The samples from Waihaha stream, one of the headwaters of the Tongariro River (Table 5.1) had very low abundances, with all taxa being considered rare. Consequently, this stream's common component was excluded from

analyses on community structure. Statistical differences between the communities in the two network positions were evaluated with Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001), based on Bray-Curtis distances with 9999 permutations. As the 12 streams belonged to three basins, these were included as an additional independent variable.

Species from each assemblage, indicative of the network position, were determined with the indval function from the *labdsv* package (Roberts, 2016) with 9999 iterations. A taxon's indicator value is the product of its specificity (relative abundance of a taxon within a group of samples compared to other groups of samples) and fidelity (relative frequency of a taxon occurrence in a group of samples) (Gogina et al., 2016). A good indicator taxon will be restricted to a group of samples and will be frequent within it (Cáceres et al., 2012). Indicator value ranges between zero and one and is maximised when a taxon is abundant in every sample of only one group.

To examine correlations between the communities and their environment, Mantel tests were performed. Community dissimilarity matrices were generated for each assemblage for log(x+1) transformed data, using Bray-Curtis distances. Two explanatory distance matrices were generated using Euclidean distances, one for environmental distance that used the habitat data, and one for overland distance (the straight distance as the crow flies, between two sampling sites) that used the sampled sites' coordinates. We used overland distances because the three catchments are not connected through waterways: Mangawhero and Whanganui flow into the sea and Tongariro into Lake Taupō. Environmental variables were spatially structured, so we also run partial Mantel tests to evaluate the effect of environmental distance while controlling for overland distance and vice versa, as spatial autocorrelation can inflate type I error rates in species-environment relationships (Kärnä et al., 2015; Peres-Neto & Legendre, 2010).

5.3 Results

5.3.1 Headwater and mainstem habitat

Headwater streams (HW) differed from the mainstem sites (MS) in that they were narrower and shallower, with lower flows, lower temperature, and their substrate was covered less by periphyton, mostly thinner forms, and more bryophytes. Stream banks were to a greater extent undercut, while canopy cover above the streams was denser than in the mainstem and their riparian zone was also covered to a greater extent by vegetation (Table 5.2, Fig. 5.2). In a PCA there was a clear distinction between habitat characteristics of the HW and MS sites (Fig. 5.3), with MS being characterised by higher algal presence, while HW had higher slope, higher velocity, more native riparian forest, larger substrate and were found at higher altitude. Environmental and overland distances were weakly correlated (Mantel r = 0.6, P < 0.003).

Figure 5.2: a) Headwater stream with closed canopy (Mangaeteroa), b) Headwater stream with open canopy (Mangatoetoenui), c) Mainstem river (Whanganui), sampled in February 2018, central North Island of New Zealand.

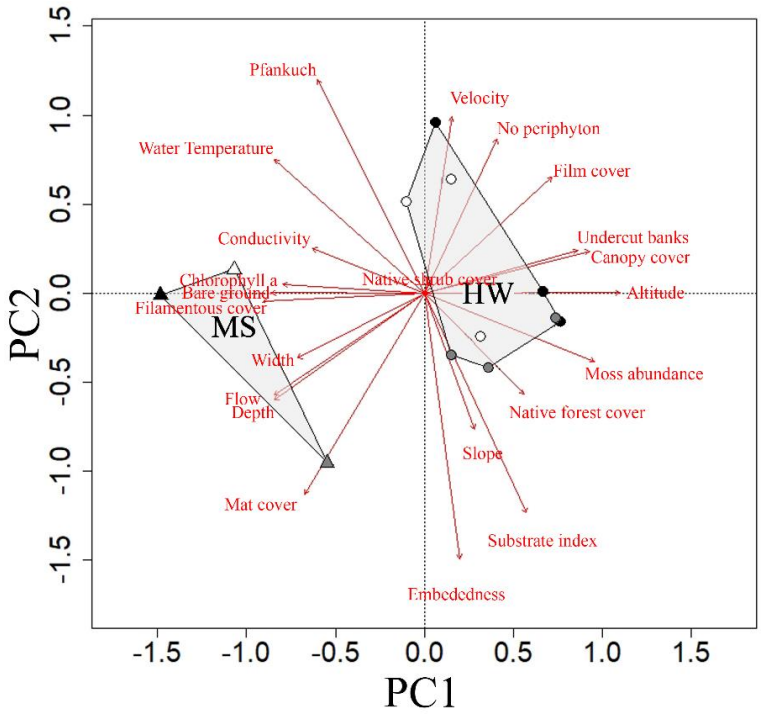

Figure 5.3: PCA ordination of habitat characteristics from three headwater streams (HW) and one mainstem river (MS) sampled in each of three basins in and around Tongariro National Park, New Zealand, February 2018. Arrow lengths show correlation strength between environmental variables and principal components

5.3.2 Headwater and mainstem biodiversity

In total 117 taxa were identified from the 12 sampling sites (Appendix D: Table S5.1), 107 from nine HW (mean = 52) and 73 from three MS sites (mean = 46). Three quarters of these were on average considered rare in either position within the stream network. No differences were found between taxonomic richness of the HW and the MS, whether the total communities were examined or any of their components and dispersal groups (Table 5.3 – Fig. 5.4). Abundance differed for the total communities and their common components, when all dispersal groups were pooled and when only PaTe macroinvertebrates were considered, but for this metric MS sites reached higher values than HW (MS mean = 395 and 377 respectively and HW mean = 152 and 135 respectively) (Table 5.3 – Fig. 5.5). When richness was rarefied to the lowest abundance (144 individuals in Waihaha Stream, tributary of the Tongariro River), HW streams

hosted higher numbers of taxa (mean = 27) in comparison to the MS sites (mean = 19). Diversity differed statistically between HW and MS sites for the complete communities, which were more diverse in HW (mean = 17) than in MS sites (mean = 10), as were the PaTe assemblages (HW mean = 9, MS mean = 5) (Table 5.3 – Fig. 5.6). Communities in HW streams were more even than communities in MS sites, with a 13% difference when the complete communities were assessed, and 16% when only the PaTe or AcTe assemblages were assessed (Table 5.3 – Fig. 5.7).

Beta-diversity was not found to differ among HW and MS samples for any of the community assemblages, irrespective of the rarity component or the dispersal group examined (Table 5.4). Species replacement and richness difference explained similar percentages of the variation of the common assemblages' β-diversity. But for the rare assemblages, species replacement explained more of the β-diversity variation (77 – 85%) than the species richness difference did (15 – 23%), except for the PaAq group where both components explained similar variation percentages. The relative contribution of each β-diversity component in the total communities appeared to be driven mainly by the common taxa. The species richness difference component of beta-diversity did not differ between HW and MS, but species replacement was higher in the MS habitats for the total communities and their common components. In both HW and MS communities the common assemblages' replacement variability (distance to the median for HW: 0.18, and for MS: 0.45) drove that of the total communities (HW: 0.18, MS: 0.44), while the rare assemblages were much more variable (HW: 0.46, MS: 0.56), but without clear effect on the total communities. The same pattern was also observed for the PaTe and AcTe assemblages. The variability of the richness difference component of the total community (HW: 0.21, MS: 0.03) appeared to result from the combination of the more variable

common assemblages (HW: 0.29, MS: 0.09) and the less variable rare assemblages (HW: 0.02, MS: 0.03).

Table 5.3: Biodiversity metrics of macroinvertebrate assemblages and their aerial dispersal groups, passively dispersing terrestrial adults (PaTe) and actively dispersing terrestrial adults (AcTe). Samples were collected from three headwater streams (HW) and one mainstem site (MS) in each of three catchments in the Tongariro National Park, New Zealand, February 2018. z-values and significance levels provided from comparisons between HW and MS ecosystems using Generalised Linear Mixed Models, with Gaussian distribution, network position as fixed effect and basin as random factor.

Metric†	Assemblage	Dispersal	HW				MS				
			Min	Max	Mean	SE	Min	Max	Mean	SE	z
NSp	Total	All	26	69	51.8	3.9	39	52	46.3	3.8	-1.15
	rarefied		22.9	32.2	26.5	0.9	12.8	23.1	18.9	3.1	**-3.92** ***
		PaTe	10	32	24.2	2.0	20	27	23.0	2.1	-0.38
		AcTe	15	32	25.2	1.7	14	24	20.3	3.2	-1.49
	Common	All	1	20	12.7	2.0	10	14	12.3	1.2	-0.14
		PaTe	1	12	6.6	1.0	5	9	7.0	1.2	0.26
		AcTe	0	11	5.6	1.1	3	5	4.3	0.7	-0.80
	Rare	All	25	50	39.1	2.3	29	38	34.0	2.7	-1.25
		PaTe	9	24	17.7	1.4	15	18	16.0	1.0	-0.60
		AcTe	15	23	19.7	0.8	11	19	16.0	2.5	-1.27
Abundance	Total	All	28.8	685.6	340.2	78.1	500.8	1204.8	738.1	233.4	**3.11** **
		PaTe	15.0	397.2	151.9	39.5	151.0	651.2	394.9	144.5	**2.59** **
		AcTe	13.4	495.6	172.8	46.3	125.8	275.4	218.9	46.9	0.73
	Common	All	10.0	646.2	301.4	76.8	460.2	1165.6	697.0	234.3	**3.13** **
		PaTe	10.0	373.6	135.0	38.1	130.8	633.6	376.9	145.2	**2.61** **
		AcTe	0.0	477.4	151.8	46.5	99.0	258.2	199.4	50.4	0.75
	Rare	All	18.8	54.4	38.7	3.3	39.2	43.4	41.1	1.2	0.43
		PaTe	5.0	25.2	16.8	2.3	16.2	20.2	18.0	1.2	0.31
		AcTe	13.4	28.2	21.0	1.5	14.4	26.8	19.5	3.8	-0.53
EfNSp	Total	All	11.4	24.7	16.5	1.3	6.8	12.3	9.7	1.6	**-3.16** **
		PaTe	3.7	11.8	8.7	0.9	2.9	8.6	5.4	1.7	**-2.03** *
		AcTe	5.3	12.5	8.0	0.7	2.0	9.6	5.5	2.2	-1.75
	Common	All	1.0	13.3	9.1	1.2	5.6	8.6	7.0	0.9	-1.09
		PaTe	1.0	7.1	5.1	0.6	2.5	5.5	3.9	0.9	-1.06
		AcTe	1.0	7.1	4.1	0.6	1.5	4.5	3.1	0.9	-0.91
	Rare	All	15.5	33.0	25.1	1.6	19.8	24.7	21.7	1.5	-1.27
		PaTe	7.2	16.8	12.4	1.0	8.1	10.8	9.6	0.8	-1.81
		AcTe	8.7	14.1	12.3	0.6	8.2	14.3	11.6	1.8	-0.57
REv	Total	All	0.67	0.82	0.71	0.02	0.52	0.65	0.58	0.04	**-4.10** ***
		PaTe	0.56	0.79	0.67	0.03	0.36	0.70	0.51	0.10	**-2.54** *
		AcTe	0.53	0.80	0.65	0.03	0.26	0.71	0.49	0.13	**-2.21** *
MCI			121.9	135.0	128.4	1.7	107.6	124.4	118.7	5.6	**-2.53** *
QMCI			6.2	8.0	7.1	0.2	3.7	6.2	4.6	0.8	**-4.80** ***

† NSp = Number of species; EfNSp = Effective number of species; REv = Relative evenness; MCI = Macroinvertebrate Community Index; QMCI = Quantitative MCI

Significance levels: * < 0.05, ** < 0.01, *** < 0.001

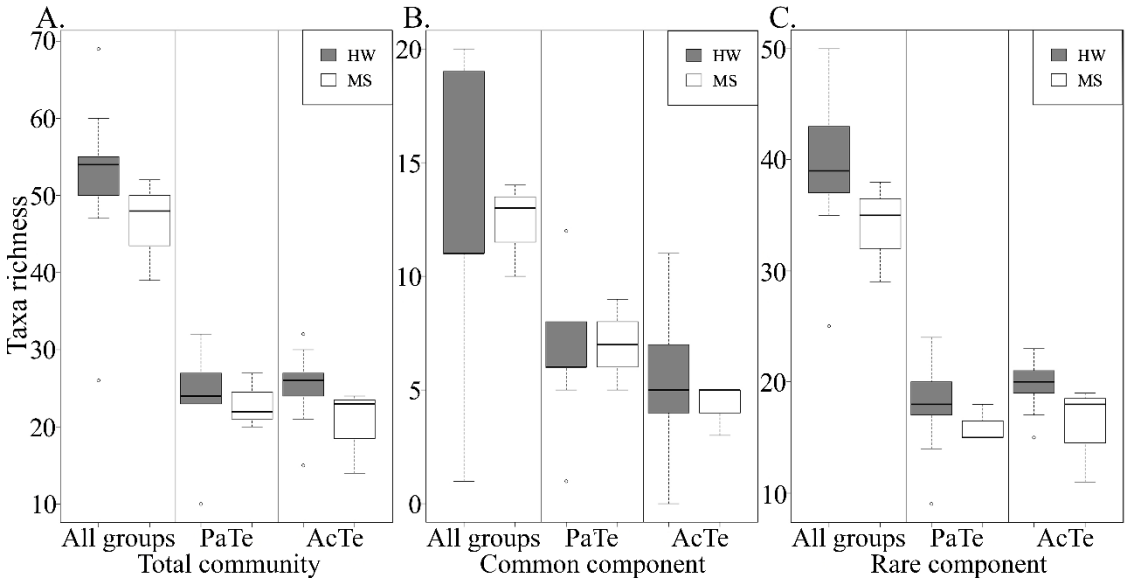

Figure 5.4: Taxa richness for the (A) total assemblages and (B) their common and (C) rare components, distinguishing groups of macroinvertebrates whose flying adults disperse through the air passively (PaTe) or actively (AcTe). Surber samples were collected from three headwater streams (HW) and one mainstem river (MS) in each of three basins in the Tongariro National Park, New Zealand, February 2018. Note differences in the scale of the y-axes. No significant differences were found between HW and MS assemblages.

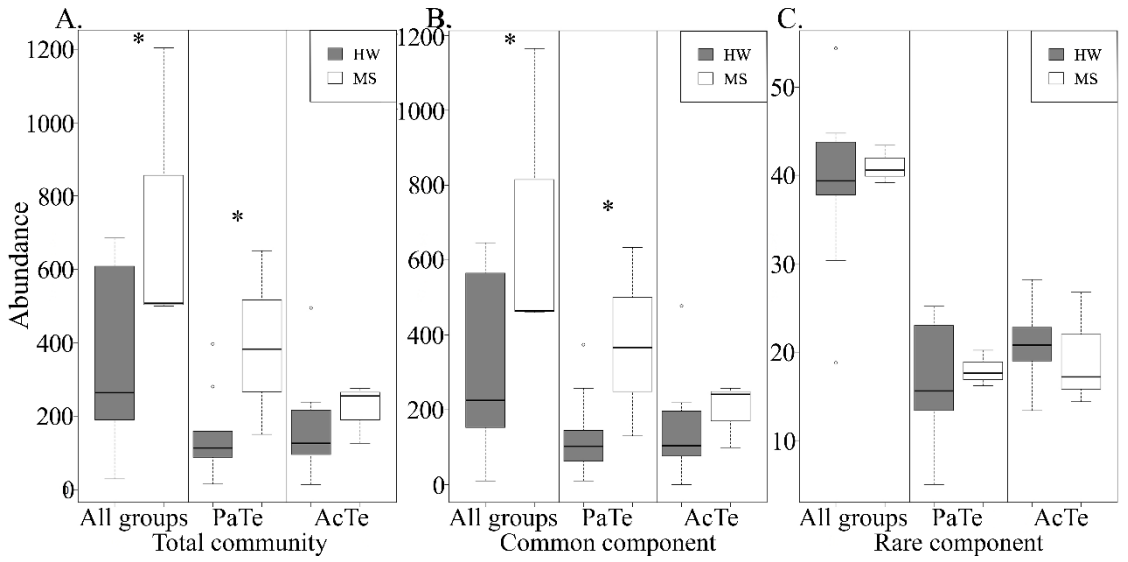

Figure 5.5: Macroinvertebrate abundance for the (A) total assemblages and (B) their common and (C) rare components, distinguishing groups of macroinvertebrates whose flying adults disperse through the air passively (PaTe) or actively (AcTe). Surber samples were collected from three headwater streams (HW) and one mainstem river (MS) in each of three basins in the Tongariro National Park, New Zealand, February 2018. Note differences in the scale of the y-axes. Significant differences are indicated with an asterisk "*" ($P < 0.05$).

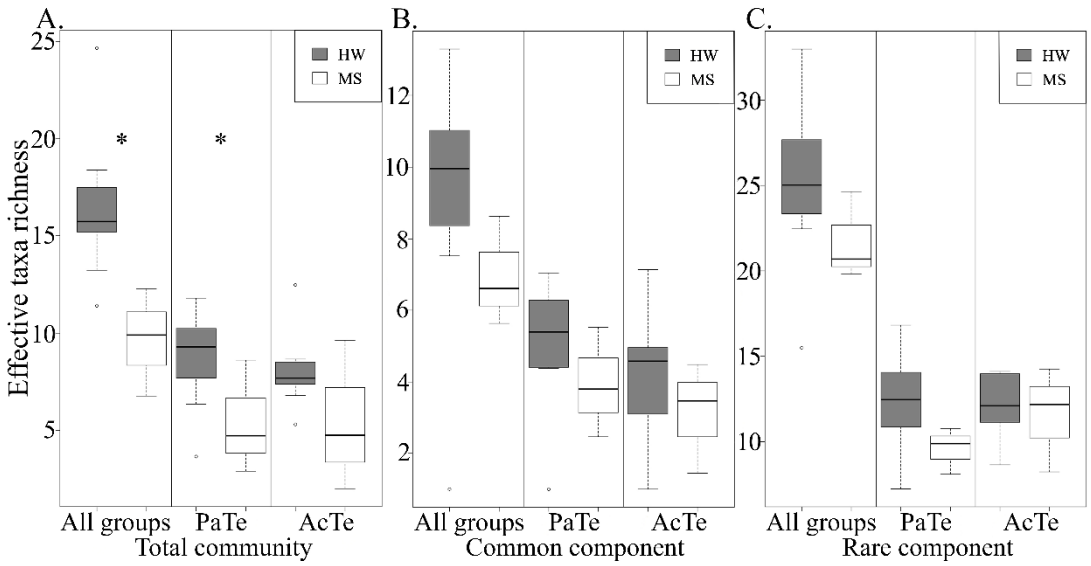

Figure 5.6: Effective taxa richness for the (A) total assemblages and (B) their common and (C) rare components, distinguishing groups of macroinvertebrates whose flying adults disperse through the air passively (PaTe) or actively (AcTe). Surber samples were collected from three headwater streams (HW) and one mainstem river (MS) in each of three basins in the Tongariro National Park, New Zealand, February 2018. Note differences in the scale of the y-axes. Significant differences are indicated with an asterisk "*" (P>0.05).

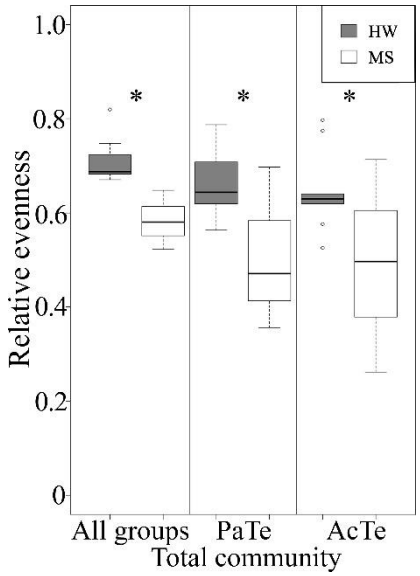

Figure 5.7: Relative evenness of the total assemblages, distinguishing groups of macroinvertebrates whose flying adults disperse through the air passively (PaTe) or actively (AcTe). Surber samples were collected from three headwater streams (HW) and one mainstem river (MS) in each of three basins in the Tongariro National Park, New Zealand, February 2018. Significant differences are indicated with an asterisk "*" (P>0.05).

Table 5.4: Assessment of β-diversity and its components (taxa replacement and nestedness) via analysis of multivariate homogeneity of group dispersions. Euclidean distances between principal coordinates of sampling sites and group medians were used, and comparison between headwater streams (HW) and mainstem sites (MS) for log(x+1) transformed abundance data of the total communities, their common and rare components and the differently dispersing groups within each assemblage. Three HW streams and one MS site were sampled in February 2018 from each of three drainage basins in and around Tongariro National Park, New Zealand.

			β – diversity				Replacement				Richness difference			
Assem-blage	Dispesal mode †	df	Distance to median		F	Relative contri-bution	Distance to median		F	Relative contri-bution	Distance to median		F
			HW	MS			HW	MS			HW	MS	
Total	All	1,10	0.32	0.35	0.11	0.60	**0.18**	**0.44**	**5.57***	0.40	0.21	0.03	1.88
	PaAq	1,10	0.53	0.55	0.01	0.17	0.21	0.001	3.66	0.83	0.42	0.57	0.57
	PaTe	1,10	0.34	0.37	0.10	0.60	0.22	0.38	1.56	0.40	0.20	0.07	0.84
	AcTe	1,10	0.29	0.31	0.05	0.53	0.19	0.24	0.28	0.47	0.21	0.13	0.30
Common	All	1,10	0.39	0.38	0.02	0.50	**0.18**	**0.45**	**5.68***	0.50	0.29	0.02	2.65
	PaAq	-	-	-	-	-	-	-	-	-	-	-	-
	PaTe	1,10	0.40	0.42	0.03	0.50	0.21	0.32	0.70	0.50	0.27	0.09	1.07
	AcTe	1,9	0.37	0.37	0.03	0.50	0.19	0.20	0.03	0.50	0.26	0.18	0.59
Rare	All	1,10	0.47	0.52	0.82	0.85	0.46	0.56	2.29	0.15	0.09	0.03	0.72
	PaAq	1,10	0.56	0.64	0.25	0.45	0.29	0.30	0.01	0.55	0.26	0.42	1.32
	PaTe	1,10	0.49	0.57	2.21	0.77	0.40	0.61	4.52	0.23	0.17	0.03	2.54
	AcTe	1,10	0.46	0.47	0.03	0.83	0.47	0.37	1.44	0.17	0.07	0.15	1.50

† PaAq = Aquatic passive dispersers; PaTe = Flying passive dispersers; AcTe = Flying active dispersers

Significance levels: * < 0.05, ** < 0.01, *** < 0.001

5.3.3 Community structure

Community structure differed among basins only for the PaAq assemblages. It differed between the network positions for the complete communities, their AcTe insects, and the PaTe and AcTe insects of the common components (Appendix D: Table S5.2). The species that were most indicative of the headwater communities (Table 5.5), were the stoneflies *Megaleptoperla grandis*, *Austroperla cyrene* and *Zelandoperla decorata* and the mayfly *Deleatidium myzobranchia*, all belonging to the AcTe dispersal group. Mainstem communities were mostly characterised by midges of the Orthocladiinae subfamily and the Tanytarsini tribe, which belonged to the PaTe dispersal group, and by the caseless caddisflies *Costachorema xanthopterum* and *Hydrobiosis umbripennis* group, of the AcTe dispersal group. The common community component in headwater

streams was indicated only by *Z. decorata*, while the rare component only by *M. grandis*. The common component of the mainstem communities was indicated by the chironomid taxa Tanytarsini and Orthocladiinae, while the caddisflies *H. umbripennis* gr. and *C. xanthopterum* were indicative of the rare component.

Table 5.5: Indicator Value Analysis of macroinvertebrate communities, and their common and rare components, from headwater streams (HW) and mainstem river sites (MS) in and around the Tongariro National Park, New Zealand, February 2018.

Assemblage	Taxa	Dispersal Group †	NetPos	IndVal
Total	*Megaleptoperla grandis*	AcTe	HW	1.00***
	Deleatidium myzobranchia	AcTe	HW	0.80*
	Austroperla cyrene	AcTe	HW	0.78*
	Zelandoperla decorata	AcTe	HW	0.74*
	Tanytarsini	Pate	MS	0.79*
	Costachorema xanthopterum	AcTe	MS	0.67*
Common	*Zelandoperla decorata*	AcTe	HW	0.67*
	Orthocladiinae C	PaTe	MS	0.87*
	Tanytarsini	PaTe	MS	0.86***
	Orthocladiinae D	PaTe	MS	0.67*
Rare	*Megaleptoperla grandis*	AcTe	HW	0.89*
	Hydrobiosis umbripennis group	AcTe	MS	0.83*
	Costachorema xanthopterum	AcTe	MS	0.67*

† PaTe = Passively flying dispersal group; AcTe = Actively flying dispersal group
Significance levels: * < 0.05, ** < 0.01, *** < 0.001

5.3.4 Community in correlation with the environment

Mantel and partial Mantel tests showed that environmental distances were correlated with the biological dissimilarities of the complete communities and the assemblages of the passively air-dispersing insects (Table 5.6). This pattern was present in the common component of the communities only for the PaTe insects. Actively air-dispersing insects' dissimilarities were shown to correlate significantly with both environmental and overland distances. But these correlations were diminished when we controlled for the overland and environmental distances respectively. The biological distances of the rare component correlated only with the physical distances, but when the environmental

distances were controlled for, this correlation disappeared as well. However, PaAq species were correlated only with the overland distances for both total communities and their rare components (the common component's correlation could not be assessed).

Table 5.6: Mantel test for log(x+1) transformed abundance data based on Bray-Curtis biological dissimilarity matrices, from samples collected in headwater and maistem streams in and around the Tongariro National Park, New Zealand, February 2018. Tests were performed for overland distances, environmental distances, overland while controlling for environmental and environmental while controlling for overland.

Assemblage	Dispersal group †	Overland	Environment	Overland (partial)	Environment (partial)
Total	All	0.37	**0.44***	0.16	**0.29***
	PaAq	**0.37****	0.11	**0.38****	-0.14
	PaTe	0.31	**0.45***	0.06	**0.34***
	AcTe	0.34	0.38	0.15	0.24
Common	All	0.23	0.33	0.05	0.25
	PaAq	-	-	-	-
	PaTe	0.22	**0.4***	-0.04	**0.37***
	AcTe	**0.39***	**0.39***	0.22	0.22
Rare	All	**0.4***	0.37	0.25	0.17
	PaAq	**0.49*****	0.14	**0.51*****	-0.22
	PaTe	0.25	0.25	0.13	0.13
	AcTe	0.29	0.32	0.13	0.2

† PaAq = Aquatic passive dispersers; PaTe = Flying passive dispersers; AcTe = Flying active dispersers

Significance levels: * < 0.05, ** < 0.01, *** < 0.001

5.4 Discussion

Lotic ecosystems' dendritic structure, naturally restricted connectivity and their macroinvertebrates' limited dispersal potential can shape biodiversity patterns and render those organisms vulnerable to human disturbance (Altermatt et al., 2020; Strayer & Dudgeon, 2010). Lotic metacommunities can be structured by their local environment and dispersal processes, defined by the location within the network and the species' traits, which can vary among common and rare species (Spitale, 2012; Thompson & Townsend, 2006). These relationships can influence the success of conservation, management and

restoration actions (Anderson & Hayes, 2018). This study evaluated the effect of stream network position and dispersal mode on assemblage structure of common and rare benthic macroinvertebrates, distinguished based on their relative abundance in each sample.

5.4.1 Effect of network position on the biodiversity of common and rare assemblages

Higher numbers of individuals were collected in MS sites than in HW, as would be expected in larger and better-connected habitats (Altermatt et al., 2013; Anderson & Hayes, 2018; Castro et al., 2019). This difference was evident for the PaTe insects and the complete communities (upon incorporation of the PaAq invertebrates) and could be related to their more limited dispersal potential. Downstream dispersal towards the MS sites takes place mostly via larval drift and to a lesser extent via adult flight. Upstream dispersal relies almost entirely on flight for insects and upstream crawling or animal vectors for non-flying invertebrates. As AcTe species are capable of covering longer distances flying upstream, their abundances would differ less between HW and MS than would the PaTe abundances (Cucherousset et al., 2008; Lancaster et al., 2020; Siqueira et al., 2020).

Higher abundances of macroinvertebrates usually lead to higher richness (Carrara et al., 2014; Cucherousset et al., 2008; McGill et al., 2007). Surprisingly, no difference was found between HW and MS taxa richness. Despite the small sample size, taxonomic richness in headwater streams was consistently higher or at least equal to that of mainstem sites, the only exception being Waihaha stream, headwater stream of the Tongariro River, which hosted low numbers of benthic invertebrates. The pattern between HW and MS was amplified when the number of macroinvertebrates collected was taken in account. Rarefied richness was clearly higher in HW streams. Mainstem sites in the Mangawhero

and Whanganui River catchments outside the national park may have been affected by the low-intensity farming in the area, however this would not be expected to lead to drastically lower richness (Tonkin et al., 2013). The Tongariro MS site has only little human activity within its catchment, but its richness was still close to that of the HW. Flooding of streams and rivers is a frequent disturbance in Aotearoa New Zealand (Winterbourn et al., 1981) and might have been responsible for the observed patterns. Floods disturb the streambed and remove periphyton and macroinvertebrates. In open canopy streams, periphyton is the main food source for macroinvertebrates, so they rely on its development before they can recolonise a disturbed reach. In closed canopy streams they can utilise a wider variety of allochthonous food sources such as leaf litter falling from the canopy, the provision of which remains unaffected by the flood (Tonkin et al., 2013). Consequently, community effects of flood disturbance are stronger in open canopy streams (Death, 2002; Death & Zimmermann, 2005; Tonkin et al., 2013). Our HW streams were a balanced mixture of closed and partly or entirely open canopy sites and all the MS sites were open. Absence of canopy cover, along with the higher frequency of floods in MS compared to HW streams (Benda et al., 2004), can render MS more susceptible, as a group, to disturbance. The MS were probably lightly enriched with nutrients from their farmed catchments, in contrast to the HW which were in the pristine environment of the national park. Nevertheless, they might had still needed more time to recover from disturbance and reach normal productivity and richness levels compared to the HW (Tonkin et al., 2013).

Surprisingly, diversity and evenness were higher in HW than in MS for the total communities, in contrast to what was expected (Altermatt et al., 2013; Anderson & Hayes, 2018; Carrara et al., 2012). Similar differences were observed for the diversity of the PaTe assemblages, and also (even though smaller and not significant) for the diversity of the

common and rare assemblages. The inclusion of rare taxa did not blur or mask diversity patterns observed for the common taxa (Marchant, 1999, 2002), instead, it elucidated differences between the diversity of HW and MS communities that would otherwise have been missed. These results contradict the expectations of the River Continuum Concept (RCC – Vannote et al., 1980), which predicts that headwater streams (1^{st} – 2^{nd} order) will host less diverse communities that mid-sized streams (3^{rd} to 5^{th} order). However, the HW streams in our study were between 1^{st} and 4^{th} order, while the MS rivers were 5^{th} and 6^{th}. Thus, they did not strictly correspond to the groups defined by the RCC. But this combination of stream orders in each group would be expected to give equivalent levels of diversity between HW and MS. The RCC has been shown to not describe New Zealand streams adequately because of the commonly open canopy habitat, low organic inputs and absence of shredder species from HW (Cowie, 1983; Winterbourn et al., 1981). Lower diversity and evenness in MS might be related to their more frequent flooding events. Tonkin et al. (2013) found that diversity and evenness were higher in closed canopy streams in the same area, and this difference was related to streambed stability and disturbance, but not productivity. In our study, streambed stability did not differ between HW and MS, but streambed cover by different types of algae was higher in MS. Flood disturbances remove food resources and animals from the habitat, and shift the community towards earlier succession stages, which, with sufficient recovery of resources, are characterised by the dominance of early colonisers (Death, 2002; Death & Zimmermann, 2005). With regards to the dispersal groups, the greater similarity of diversity patterns between the entire assemblage and the PaTe dispersers but not as much with the AcTe, could be related to their dispersal ability. AcTe are less dispersal limited than PaTe and thus able to colonise available habitats more quickly post-disturbance in both network positions.

Inclusion of rare taxa facilitated the distinction between communities found in HW and MS. In a small-scale study such as this, the common taxa components can be expected to be relatively similar in different parts of the network (Cao et al., 2001), and despite the rare components' high variability, their combination can offer clearer patterns. The flying dispersers of the common components also differed between HW and MS, while the PaAq assemblages differed between catchments. The three catchments were located on different sides of the national park but close as the crow flies. PaTe and AcTe insects are able to disperse overland using the stream network as a series of stepping-stones (Tonkin et al., 2015). For PaAq assemblages to be similar across catchments, animal vectors would be necessary for overland dispersal, but this route is unlikely to consistently reintroduce PaAq populations in these ecosystems, which are also commonly disturbed by floods.

Contrary to predictions, beta diversity did not differ between HW and MS. Metacommunity theory would predict β-diversity to be higher among less-connected ecosystems and/or higher altitudes, i.e. headwaters (Castro et al., 2019; Swan & Brown, 2014). The taxa turnover component of β-diversity was found to be higher for MS sites, possibly suggesting higher variation amongst them than amongst HW communities (Legendre, 2014). Higher turnover would be expected among the less connected HW streams (Jamoneau et al., 2018; Krynak et al., 2019), where taxa with narrower niches and those more sensitive to disturbance are usually found (Tornwall et al., 2017). The national park contains a dense network of stream ecosystems, draining several catchments. Even the HW streams are not isolated, and flying insects can easily disperse between them (Bilton et al., 2001). Higher turnover among MS streams may reflect larger differences in climate and land-cover at lower altitudes (Kärnä et al., 2015; Tonkin et al., 2013), while drifting invertebrates from the HW communities might have increased

compositional differences between MS (Siqueira et al., 2020). However, one potential confounding factor could be the small sample size of MS sites, which resulted from the limited number of catchments draining Tongariro National Park and an attempt to replicate the numerical imbalance between HW streams and MS sites that results naturally from the structure of lotic networks.

Inclusion of rare taxa did not affect the total communities' taxa turnover patterns, which were driven almost entirely by the common taxa. Rare taxa turnover did not differ between HW and MS, although there was a trend similar to that observed in the common assemblages. They also had much higher replacement than the common taxa assemblages, in contrast to Heino & Soininen (2010) who did not find differences. This difference was probably a result of our definition of rarity, based on relative abundance per sample, while Heino & Soininen (2010) defined rare taxa based on occurrence frequency. Higher replacement could indicate that rare assemblages in these streams are closely related to the local environment (Siqueira et al., 2012; Swan & Brown, 2014). Because of our definition of rarity, the same species are common in some sites and rare in others. Thus, a close relationship of the rare taxa with the environment could reveal specific conditions that are not ideal for the development of large populations on a species-by-species basis.

5.4.2 Effect of local environment and dispersal processes on community structure

Except for the dispersal limited PaAq, which were closely linked with overland distances, community structure of all other groups were linked most strongly with local environmental conditions, not distances among streams. Brown & Swan (2010) found communities in headwater streams to be entirely driven by their local environment in contrast to mainstem sites, where both the local environment and dispersal processes were

important. Nicacio & Juen (2018) found weak dispersal effects on community structure and only at broad spatial scales. The three catchments are on opposing sides of the volcanic massif and thus separated by a steep ecological gradient which must act as a dispersal barrier. However, overland connectivity is good, as the landscape is drained by numerous headwater streams. The absence of strong effects on community structure by this dispersal limitation suggests that at such small scales the local environmental conditions play the biggest role in structuring the communities (Grönroos et al., 2013; Mendoza et al., 2018).

5.4.3 Effect of species sorting on common and rare assemblages

Community structure was found to be driven more by the local environment of the sampling sites, than by distances among them as a proxy for dispersal processes. However, when the common and rare components were analysed separately, there was no clear consensus as to the main driver of their structures.

The common assemblages were not shown to be structured either by the local environment or dispersal processes. There was, however, a mild, albeit non-significant, connection to the former. Because of the small study area and the pristine or near pristine condition of the streams, it is possible that the common species were both abundant and so widespread across the area that they did not differ between sites (Cao, Bark, et al., 1997; Cao et al., 2001; Jiang et al., 2014). Thanks to their more widespread presence, common species can also recolonise available habitats post-disturbance faster than rare ones (Sarremejane et al., 2018). This process was pronounced by the designation of the stronger dispersing AcTe species as indicative of the relatively more isolated HW and the weaker dispersers PaTe species indicative of better connected MS.

The rare assemblages showed some spatial structure, but when environmental variation was controlled for, the effect disappeared. Sgarbi & Melo (2018) also found no indication of spatial configuration in rare assemblages. Based on our rarity definition, the same species might be common or rare at different sites. Consequently, the rare components will be partially related to non-ideal micro-habitat conditions and stochastic disturbances. The study streams were in pristine or near-pristine condition, so non-ideal conditions that would render a species rare in a stream would have a rather narrow range. This, along with the spatial structure of the environmental variables could affect the spatial structure of the rare components as well. But this effect was not strong, as all species indicative of the rare assemblages were AcTe in both network positions. These species are stronger dispersers than PaTe, and they can follow environmental gradients more closely. Behavioural traits can also play a role in determining the local rarity of a species and the environmental or dispersal processes driving it; for example, blood-feeding insects (e.g. Simuliidae) will actively look for their hosts and this will affect their distribution in the landscape (McCreadie & Adler, 2019). Despite both components' weak relations to either environmental or spatial drivers, the combination of rare and common taxa revealed stronger connections between the community and the environment, indicating the importance of their inclusion in the study.

5.4.4 Effect of species sorting on actively and passively flying insects

Stronger dispersers are generally expected to be associated more strongly with environmental gradients, while weaker dispersers to be affected by both environmental conditions and spatial configuration (Li et al., 2019). PaTe assemblages in our streams were structured more by the local environment than the streams' spatial configuration. Interestingly, AcTe assemblage structure was not related more strongly to either

environmental or spatial patterns. AcTe species of the common assemblages appeared to be independently related to both environmental conditions and spatial configuration of the sampling sites. However, when each of these factors was controlled for its correlation with the other factor, both effects disappeared, and none of the two factors appeared to independently affect community structure. As there were no gradients that could structurally dominate community structure (e.g. disturbance), communities might have been driven by the interaction of the local environment and dispersal processes. The dense stream network around the national park might enable all community components and both aerial dispersal groups to find suitable habitats, without having to cover long distances and overcome natural obstructions (apart from the central volcanic massif) or human-degraded streams (Thompson & Townsend, 2006). PaTe species could thus have intermediate rates of dispersal, enough to track suitable habitats, while AcTe species disperse through mass effects, masking the species sorting effects (Kärnä et al., 2015). An alternative or complementary explanation could be that AcTe comprise more generalists, which are more flexible in their correlation with environmental conditions, while PaTe comprise more specialists and correlate more strongly with the environmental conditions (Pandit et al., 2009).

The more unobstructed dispersal of AcTe species in comparison to PaTe species is also supported by AcTe species being consistently indicative of HW streams, while MS rivers had both AcTe and PaTe species. AcTe species, as stronger fliers, can track environmental conditions even in more isolated habitats such as HW, also dispersing across terrestrial habitats in search of available suitable aquatic ones (Graham et al., 2017). Mainstem rivers, which are more central within the stream network, are characterised by both dispersal groups; AcTe species are able to track available habitats

with even lower dispersal limitation, and PaTe species take advantage of the increased dispersal potential in the better-connected sites to establish in new habitats.

5.4.5 Concluding remarks

The present study did not identify clear differences between rare taxa assemblages in headwaters and mainstems and neither were those assemblages strongly structured by the local environment or the distances among sites. However, inclusion of rare taxa in analyses along with the common ones did not obscure, and even strengthened/clarified weak patterns of the common components. Although species sorting is considered to be the main structuring force of macroinvertebrate metacommunities, the spatial and temporal scale of a study, the taxonomic group(s) it focuses on and changes in the stream network structure and connectivity, might alter the relative importance of environmental conditions and dispersal processes (Heino, 2013; Sarremejane, Cañedo-Argüelles, et al., 2017; Tonkin, Death, et al., 2018). Such changes might reduce the sizes of populations, rendering them more susceptible to future environmental changes and stochastic events (Siqueira et al., 2020). The natural asynchrony of life history patterns for Aotearoa New Zealand stream macroinvertebrates (Winterbourn, 1997) might increase metacommunity stability, enhancing persistence against such changes (Wilcox et al., 2017). However, conservation measures focusing on freshwater ecosystems also need to account for the particular structure of freshwater networks and the factors driving the formation of freshwater assemblages. Conservation management programmes often require artificial breaks in the area of interest for practical purposes, especially at larger scales (Jones & Schmidt, 2018). But for macroinvertebrate assemblages a catchment approach can be more appropriate, especially in small scales, such as this study. Such an approach will manage and protect headwater streams (which host variable communities and hold greater

potential for improvement of biodiversity in downstream reaches post-disturbance – Swan & Brown, 2017), mainstem reaches (which host diverse communities and facilitate connectivity between headwater streams) and will ensure connectivity both overland and via the watercourse, for adult aquatic insects and benthic macroinvertebrates respectively.

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Chapter 6 - Synthesis

Rare taxa comprise a disproportionately large component of taxa richness in biological communities (Gaston, 1994). However, they are commonly excluded from community studies on the grounds they create too much statistical noise in multivariate analyses and/or provide redundant information (Gauch, 1982; Marchant, 1999, 2002). The effect of this exclusion on analyses of lotic benthic macroinvertebrate communities has not been extensively investigated and was the focus of this thesis. This was accomplished by: i) assessing the effect of rare taxa exclusion on stream biomonitoring tools used in Aotearoa New Zealand, ii) assessing the effect of sampling method and life stage on biodiversity patterns of rare taxa, iii) examining the local habitat factors linked with the structure of the common and rare community components, and iv) assessing the effect of location within the stream network and dispersal mode on biodiversity patterns of common and rare taxa.

In chapter two, I found that exclusion of rare taxa will not heavily distort patterns in community structure, but can have a significant effect on biomonitoring indices. This effect was stronger on the Macroinvertebrate Community Index (MCI), which uses presence-absence data, while the abundance-based Quantitative MCI was relatively unaffected. Higher percentages of streams were misclassified by the MCI as greater numbers of taxa were excluded. When taxa were excluded based on their relative abundance in their respective samples, misclassifications were equal parts upgrades and downgrades. When exclusions were applied with regards to the whole study, higher quality streams were usually designated lower quality status, while low quality streams were only minimally affected. Exclusion of rare taxa sometimes weakened the relationship between anthropogenic stressors such as nitrogen and the MCI, and even masked the relationship between MCI and phosphorus, and between QMCI and nitrogen.

In chapter three, I showed that different sampling methods will collect caddisfly communities with different rare components from pristine streams and for a complete biodiversity inventory of a site we need to employ more than one method. Surber samples from riffle habitats gave the richest assemblages, but kick-nets can be used in more variable habitat patches and can collect taxa not found in riffles. I also collected adult insects with UV-light traps and SLAM traps, because they can be identified to species level (Smith, 2014). Both types of traps collected assemblages of similar diversity, but UV-light traps were much more efficient. Benthic samples require many more individuals than the trap samples to describe similar levels of biodiversity, but much less time in the field. Adult caddisfly samples can supplement biodiversity inventories that are based on benthic samples but cannot replace them.

In chapter four, I showed that inclusion of rare taxa can be important in clarifying and even determining relationships between invertebrate assemblages and the environment. Even though rare taxa can be more variable than common taxa, sometimes they carried complementary information. Biodiversity metrics of the common and rare components were related to the same environmental variables, mostly differing in strength, whether the focus was on the entire benthic assemblages, benthic caddisflies or adult caddisflies. The relationships of the assemblages' structure with their environment differed for common and rare taxa, however the inclusion of rare taxa revealed more relationships, and when focusing on smaller assemblages, like the caddisflies, it even strengthened the correlation with the environment.

In chapter five, I showed that although rare taxa seemed unrelated to local environmental variables or dispersal processes across the stream network, their inclusion did not mask but actually clarified patterns seen in the common taxa. While headwaters and mainstem streams hosted clearly different assemblages, mainstems were not richer

or more diverse than headwaters, as would be expected by the River Continuum Concept. This might be attributed to the wider range of stream orders comprising the HW streams in our study, in combination with potential recurrent high flows prior to sampling. In a small pristine area with a dense stream network, such as the Tongariro National Park, communities are driven mostly by the local environment and not dispersal. Moderately strong dispersers like larger adult macroinvertebrates can easily disperse through the area, while weaker dispersers are more strongly structured by the environment conditions. Description of macroinvertebrate patterns and consequent management in lotic networks would require the inclusion of rare taxa and a catchment approach to adequately cover all community components.

The concept of rarity can be approached and studied from many different aspects (Chapter 1). The use of the term "rarity" in all these conditions, does not make it a one-size-fits-all term describing the same phenomenon, driven by the same factors and comparable between different taxonomic groups or samples collected with different methods (Chapters 2, 3 and 4). It might be sensible to consider the different forms of rarity (Rabinowitz, 1981) as different phenomena. The distinction between common and rare taxa within each group of rarity definitions (e.g. site-specific, study-wide, abundance-based, occurrence-based etc.) will very likely be based on arbitrary cut-off points. However, the exact point of distinction will be of relatively little importance, whether it will be employed to answer simple biodiversity questions, or to create a model (Magurran, 2004; Siqueira et al., 2012; Chapter 2).

In Chapters 3 to 5, taxonomic rarity was defined based on the relative abundance of each taxon in each sample. This definition was selected on the grounds that in a relatively small and pristine study area without strong environmental gradients, such as the Tongariro National Park, distinguishing common and rare taxa in every single site

would reveal finely detailed patterns in the relationship between the taxa and their environment, without being confounded by stochastic high or low abundances. In a larger scale study, with a greater number of streams sampled, or in streams along a natural or human-induced environmental gradient, a different rarity definition, such as relative abundance over the whole study or occupancy percentage, could also reliably reveal patterns in the relationships between common and rare taxa and their environment, without being heavily affected by stochastic high and low abundances.

Based on our rarity definition, almost all taxa were rare in at least one site. In general, relationships between assemblages and their environment were similar for both common and rare taxa, albeit not always statistically significant. Rare components were usually more variable than the common components and showed weaker patterns or contained redundant information (Chapters 4 and 5). The common components were often adequate to describe the main patterns of biodiversity. However, when common taxa did not present clear patterns, inclusion of rare taxa was necessary to support the analysis and reveal statistically strong patterns (Chapters 2 and 5). Even when inclusion of rare taxa appeared to weaken the patterns observed for the common ones, they actually revealed a greater range of relationships with the environment, albeit not as strong (Chapter 4).

Incorporation of rare taxa in bioassessment calculations is clearly important for accurate classifications (Chapter 2). Failed assessment could indicate impact in sites where there is none and consequently direct funds and labour towards ecosystems that do not require restoration actions or even a change in management (Guareschi et al., 2017). Alternatively, good ecological status could be indicated where it is in fact deteriorating and precious time wasted until further changes are detected. Rare taxa are expected to be

the first to go locally extinct from a site and consequently, if they have been excluded from the dataset, their extinction will go unnoticed (Nijboer & Schmidt-Kloiber, 2004).

Certain factors limited the potential to extrapolate the conclusions of this thesis to more generalized suggestions about the structure of the rare lotic macroinvertebrate community components and their contribution to freshwater studies. The thesis dealt specifically with the contribution of rare taxa in the analysis stage, for fully counted data, on the grounds that if they carry complementary/important information to describe and explain the relationships of the macroinvertebrate communities to their environment, then they should be incorporated into community analyses. An important practical aspect of the use of rare taxa in freshwater studies would be to collate potential loss of information from their exclusion via subsampling during the sample processing and identification stages, with potential gains from reduced effort and time in the field and/or the lab and consequently reduction in research costs (Arscott et al., 2006). Also, as indicated by Chapter 2, the definition of rarity can have a big impact on statistical analysis. The choice of site-specific relative abundance as the criterion to define rarity in Chapters 3 to 5, while meaningful for a small study area with no strong environmental gradients, might have nevertheless missed other relationships between differently defined rare components of the communities and their environment. Additionally, snapshot samples always entail the risk of describing a non-representative state of a community, especially in highly dynamic ecosystems such as streams. This is in part counterbalanced by collecting multiple replicate samples from each site. However, repeated sampling during a year or over multiple years can shed further light on the community structure dynamics of the rare components of freshwater macroinvertebrate communities and their relationships to their environment (Resh et al., 2005). Finally, the available taxonomic knowledge for benthic macroinvertebrates in New Zealand will possibly limit the accuracy of any study focusing

on rare taxa. Rare species can comprise components of common genera, but it can be particularly difficult to distinguish the rare from the common species based on morphological characters. With the development of suitable species-level identification keys and the advances in DNA technology, this problem will be gradually addressed. However, data obtained from DNA samples will reliably document the presence of species in an ecosystem, but acquiring quantitative data will be a more difficult goal to reach (Elbrecht & Leese, 2015; Elbrecht et al., 2017).

Is information contained in rare taxa worth having in our datasets? This question might lead us to a paradox. As long as rare taxa are present in an ecosystem, the common ones might be enough to describe the relationship of their communities to the environment. We will only truly know the answer when the rare taxa are absent from nature as well as our datasets. This study showed that rare macroinvertebrate taxa do not hinder community analyses and might instead clarify patterns in the linkages between communities and their environment, or reveal additional ones. Rarity is nevertheless a very multifaceted phenomenon and reaching an overarching conclusion, irrespective of how we define rare species, might be utopic (McCreadie & Adler, 2008). Even though the debate on whether rare taxa should be accounted for in freshwater studies is not over yet, decision in favour of one approach over the other should be preceded by consideration of what will be the potential cost of skewed information for freshwater ecosystems' management and who will pay it (Doberstein et al., 2000).

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Appendices

Appendix A – Supplementary material for Chapter 2

Table S2.1a: MCI values calculated from the macroinvertebrate dataset collected for the National River Water Quality Network of New Zealand during the austral summer and autumn of 2005, and recalculated after the exclusion of rare taxa based on the criteria presented in Table 2.1.

		Site-specific									Study-wide									
	Full	Singleton	Doubleton	5indvs	10indvs	0.1%	0.5%	1%	5%	Subs200	Uniq	Singleton	Doubleton	5indvs	10indvs	0.1%	0.5%	1%	5%	Low25%
AX1	110	105	109	103	93	110	109	103	93	107	110	110	110	110	110	109	100	97	97	110
AX2	103	113	120	160	160	103	113	120	160	101	103	103	103	103	104	85	85	85	85	103
AX3	137	153	140	160		137	137	137	137	137	137	137	144	144	144	144	120	120	120	144
AX4	89	86	76	80	80	89	89	89	93	89	85	89	89	85	85	83	80	80	95	85
CH1	115	108	109	115	111	115	109	115	88	110	115	115	115	115	115	110	95	82	91	115
CH2	102	103	101	108	98	91	74	80	87	85	102	102	102	102	99	98	95	82	91	102
CH3	100	93	93	100	100	93	100	95	87	96	100	100	100	100	100	100	95	91	93	100
CH4	95	90	89	90	84	95	90	89	84	95	95	95	95	96	96	98	95	91	91	96
DN1	102	101	101	109	100	101	100	100	120	103	104	102	102	104	104	104	87	83	91	104
DN2	108	110	114	109	112	113	116	124	137	93	106	106	106	104	106	110	103	82	91	104
DN3	97	96	95	92	80	96	92	76	100	91	97	97	97	98	98	101	95	82	91	98
DN5	88	85	84	69	69	84	78	89	93	115	88	88	88	88	88	85	86	82	91	88
DN6	120	121	121	124	120	121	120	120	115	93	120	120	120	123	123	122	104	91	91	123
DN7	114	118	123	114	105	118	107	109	95	81	114	114	114	114	114	111	100	86	97	114
DN8	108	105	96	89	89	87	96	100	140	123	108	108	108	108	108	105	96	83	91	108
DN9	95	92	93	82	82	95	93	82	113	118	91	91	91	93	93	89	87	83	91	93
DN10	93	82	83	86	97	93	82	83	92	97	93	93	93	93	93	84	88	66	72	93
GS2	126	125	129	141	142	125	141	142	120	131	126	126	127	127	127	134	108	92	92	127
GS3	121	134	130	128	132	134	128	132	113	129	121	121	121	121	121	121	96	80	90	121
GS4	100	100	85	85	100	100	100	100	85	100	100	100	100	100	100	100	85	85	85	100
GY2	125	122	118	118	106	125	118	118	104	122	125	125	125	125	125	127	97	92	92	125
GY3	124	127	127	127	115	127	127	115	100	123	124	124	124	124	124	128	100	96	100	124
GY4	138	138	127	128	107	138	127	128	107	136	138	138	138	138	138	140	110	107	107	138
HM1	113	108	109	108	105	113	108	105	88	110	113	113	113	113	113	113	96	91	91	113
HM3	77	70	65	65	73	77	70	65	73	76	77	77	77	77	77	77	73	73	76	77
HM6	81	83	72	83	77	81	78	83	80	79	83	81	81	83	83	82	74	65	72	83
HV1	145	138	133	131	137	138	131	137	147	140	142	145	142	138	138	142	127	120	120	142
HV2	102	106	106	111	110	106	110	100	120	107	102	102	102	102	102	104	95	91	91	102
HV3	104	103	103	103	109	104	103	103	100	102	104	104	104	104	104	104	87	83	91	104
HV4	156	154	163	155	155	156	155	155	140	157	156	156	156	154	154	149	136	140	140	156
HV6	119	125	125	115	106	119	125	115	95	119	114	119	119	114	114	113	97	92	92	114
NN1	127	124	119	131	127	124	127	117	120	125	127	127	127	127	129	130	108	97	100	127
NN2	125	126	126	164	160	125	125	126	164	125	125	125	125	125	125	121	98	76	75	125
NN3	124	133	142	142	147	124	142	142	147	131	123	124	124	126	126	124	103	84	100	126
NN4	114	115	114	114	123	115	123	135	140	117	114	114	114	120	120	114	107	104	104	120
NN5	120	118	109	98	105	120	110	105	120	112	120	120	120	117	117	116	98	80	92	120
RO1	114	118	120	131	130	118	131	130	147	117	114	114	114	118	118	119	104	91	108	118
RO3	105	127	131	143	160	105	105	127	148	105	104	104	104	107	109	106	91	86	100	107
RO4	135	140	137	133	136	137	128	140	120	138	135	135	135	135	138	139	111	100	104	135
RO5	54	40	50	50	60	54	54	54	40	54	54	54	54	54	54	47	50	50	60	54
TK1	128	129	129	134	127	129	127	128	140	131	128	128	128	128	128	129	120	108	108	128
TK2	98	102	113	123	128	98	114	128	115	108	98	98	98	98	98	103	103	91	97	98
TK3	100	96	109	113	107	100	96	109	107	100	100	100	100	100	100	102	98	86	97	100
TK4	108	96	107	107	120	108	108	96	120	108	108	108	108	108	108	108	97	97	97	108
TK5	128	128	128	133	120	128	133	120	120	127	128	128	128	128	128	128	120	120	120	128
TK6	98	93	92	140	140	98	98	98	92	98	98	98	98	98	100	104	90	84	100	98
TU1	120	128	125	115	104	121	103	93	92	111	120	120	120	120	120	120	102	90	91	120
TU2	116	100	93	94	88	93	88	88	50	93	116	116	116	116	116	105	103	84	85	116
WA1	152	120	120	140	140	152	152	152	120	152	152	152	152	152	152	165				152
WA2	131	133	131	116	109	131	122	109	116	126	131	131	131	131	131	123	98	93	93	131
WA3	94	98	95	92	98	98	108	108	108	102	94	94	94	94	94	92	85	80	91	94
WA4	102	99	98	91	93	99	93	93	87	98	102	102	102	102	104	104	89	80	91	102
WA5	103	94	108	97	97	103	94	97	92	103	101	101	101	101	101	98	95	90	90	101
WA6	124	128	125	115	104	121	103	93	92	112	124	124	124	124	124	125	102	89	90	124
WA7	103	110	112	113	112	112	113	100	110	110	103	103	103	103	103	102	96	83	91	103
WA8	97	93	78	80	71	93	80	80	80	87	99	99	99	99	99	93	89	83	93	99
WA9	77	77	82	69	52	77	53	30	30	69	82	77	82	82	74	76	83	83	91	82
WH1	108	112	118	110	100	108	112	100	100	112	108	108	108	108	104	106	106	77	76	108
WH2	87	87	75	66	65	87	66	62	67	78	87	87	87	87	87	90	87	70	80	87
WN1	100	103	89	71	95	103	71	87	40	93	100	100	100	100	100	103	88	80	95	100
WN2	135	132	141	140	143	132	136	148	160	137	135	135	135	132	132	123	104	77	92	134
WN3	93	85	90	84	88	92	88	80	60	90	93	93	93	93	93	92	96	80	90	93
WN4	107	102	94	97	98	102	97	104	107	99	107	107	107	107	107	104	104	91	91	107
WN5	118	114	115	116	125	115	125	116	140	114	118	118	118	115	115	109	104	90	92	118

Table S2.1b: QMCI values calculated from the macroinvertebrate dataset collected for the National River Water Quality Network of New Zealand during the austral summer and autumn of 2005, and recalculated after the exclusion of rare taxa based on the criteria presented in Table 2.1.

		Site-specific									Study-wide									
	Full	Singleton	Doubleton	5indvs	10indvs	0.1%	0.5%	1%	5%	Subs200	Uniq	Singleton	Doubleton	5indvs	10indvs	0.1%	0.5%	1%	5%	Low25%
AX1	2.8	2.8	2.8	2.8	2.7	2.8	2.8	2.8	2.7	2.8	2.8	2.8	2.8	2.8	2.8	2.8	2.8	2.8	2.8	2.8
AX2	7.8	7.9	7.9	8.0	8.0	7.8	7.9	7.9	8.0	7.8	7.8	7.8	7.8	7.8	7.9	7.8	7.8	7.8	7.8	7.8
AX3	7.4	7.6	7.4	8.0		7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.5	7.5	7.5	7.5	7.2	7.2	7.2	7.5
AX4	3.3	3.3	3.1	3.0	3.0	3.3	3.3	3.3	3.2	3.3	3.2	3.3	3.3	3.2	3.2	3.1	3.1	3.1	3.2	3.2
CH1	4.5	4.5	4.5	4.5	4.4	4.5	4.5	4.5	4.2	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.3	4.3	4.3	4.5
CH2	3.7	3.7	3.7	3.7	3.7	3.7	3.7	3.7	3.8	3.7	3.7	3.7	3.7	3.7	3.7	3.7	3.7	3.7	3.7	3.7
CH3	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.6	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7
CH4	4.0	3.9	3.9	3.9	3.8	4.0	3.9	3.9	3.8	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.3	4.2	4.2	4.0
DN1	6.4	6.4	6.4	6.5	6.5	6.4	6.5	6.5	6.8	6.4	6.4	6.4	6.4	6.4	6.4	6.4	6.5	6.5	6.6	6.4
DN2	6.8	6.8	6.8	6.8	6.8	6.8	6.9	6.9	7.0	4.9	6.8	6.8	6.8	6.8	6.8	6.9	7.0	5.0	5.1	6.8
DN3	4.7	4.7	4.7	4.7	4.7	4.7	4.7	4.6	5.0	4.0	4.7	4.7	4.7	4.7	4.7	4.7	4.8	4.7	4.9	4.7
DN5	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.7	5.8	6.9	5.6	5.6	5.6	5.6	5.6	5.6	5.7	5.7	5.8	5.6
DN6	5.8	5.8	5.8	5.8	5.8	5.8	5.8	5.8	5.8	4.8	5.8	5.8	5.8	5.8	5.8	5.8	5.8	5.7	5.7	5.8
DN7	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.5	5.6	6.5	6.5	6.5	6.5	6.5	6.5	7.0	6.9	6.9	6.5
DN8	6.3	6.3	6.3	6.3	6.3	6.3	6.4	6.4	6.6	5.8	6.3	6.3	6.3	6.3	6.3	6.3	6.3	6.3	6.4	6.3
DN9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	5.2	6.5	4.9	4.9	4.9	4.9	4.9	4.9	5.0	4.9	5.1	4.9
DN10	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	3.9	6.3	4.0	4.0	4.0	4.0	4.0	3.4	3.4	3.4	3.3	4.0
GS2	6.4	6.4	6.4	6.4	6.4	6.4	6.4	6.4	6.2	6.4	6.4	6.4	6.4	6.4	6.4	6.4	6.2	6.3	6.3	6.4
GS3	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.7	7.7	7.6
GS4	5.8	5.8	5.8	5.8	6.5	5.8	5.8	5.8	5.8	5.8	5.8	5.8	5.8	5.8	5.8	5.8	5.8	5.8	5.8	5.8
GY2	4.4	4.4	4.3	4.3	4.2	4.4	4.3	4.3	4.1	4.4	4.4	4.4	4.4	4.4	4.4	4.4	3.8	3.7	3.7	4.4
GY3	3.1	3.1	3.1	3.1	3.0	3.1	3.1	3.0	2.7	3.1	3.1	3.1	3.1	3.1	3.1	3.1	2.9	2.8	2.8	3.1
GY4	5.6	5.6	5.6	5.5	5.4	5.6	5.6	5.5	5.4	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.4	5.4	5.4	5.6
HM1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.2	5.1	5.1	5.1	5.1	5.1	5.1	5.3	5.3	5.3	5.1
HM3	3.6	3.6	3.5	3.5	3.6	3.6	3.6	3.5	3.6	3.6	3.6	3.6	3.6	3.6	3.6	3.6	3.6	3.6	3.6	3.6
HM6	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	4.0	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.8	3.9	3.9
HV1	6.8	6.8	6.8	6.8	6.9	6.8	6.8	6.9	6.8	6.9	6.8	6.8	6.8	6.8	6.8	6.8	6.6	6.6	6.6	6.8
HV2	7.1	7.1	7.1	7.1	7.1	7.1	7.1	7.1	7.5	7.1	7.1	7.1	7.1	7.1	7.1	7.1	7.1	7.1	7.1	7.1
HV3	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.0	5.0	5.0	5.1
HV4	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.1	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.1	7.1	7.1	7.2
HV6	5.6	5.7	5.7	5.6	5.6	5.6	5.7	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.5	5.5	5.5	5.6
NN1	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.2	5.3	5.3	5.3	5.3	5.3	5.4	5.3	5.3	5.1	5.1	5.3
NN2	7.0	7.0	7.0	7.5	7.3	7.0	7.0	7.0	7.5	7.0	7.0	7.0	7.0	7.0	7.0	6.8	6.3	5.3	5.4	7.0
NN3	7.6	7.7	7.7	7.7	7.8	7.6	7.7	7.7	7.9	7.6	7.6	7.6	7.6	7.7	7.7	7.7	7.6	7.6	7.6	7.7
NN4	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.5	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4
NN5	5.7	5.7	5.7	5.7	5.7	5.7	5.7	5.7	5.8	5.7	5.7	5.7	5.7	5.7	5.7	5.7	5.7	5.7	5.7	5.7
RO1	6.8	6.8	6.8	6.8	6.8	6.8	6.8	6.8	6.9	6.8	6.8	6.8	6.8	6.8	6.8	4.1	4.1	4.1	6.8
RO3	7.4	7.6	7.6	7.9	8.2	7.4	7.4	7.6	8.0	7.4	7.4	7.4	7.4	7.4	7.5	7.5	6.5	6.7	6.9	7.4
RO4	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	4.8	5.2	5.1	5.1	5.1	5.1	5.1	5.1	4.8	4.8	4.8	5.1
RO5	2.6	2.5	2.6	2.6	3.0	2.6	2.6	2.6	2.5	2.6	2.6	2.6	2.6	2.6	2.6	2.5	2.6	2.6	2.7	2.6
TK1	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.1	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.0	6.9	6.9	7.0
TK2	5.2	5.2	5.2	5.2	5.2	5.2	5.2	5.2	5.1	5.2	5.2	5.2	5.2	5.2	5.2	5.2	5.2	5.1	5.1	5.2
TK3	4.6	4.6	4.6	4.6	4.5	4.6	4.6	4.6	4.5	4.6	4.6	4.6	4.6	4.6	4.6	4.5	4.7	4.4	4.4	4.6
TK4	7.4	7.5	7.5	7.5	7.7	7.4	7.4	7.5	7.7	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4
TK5	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.8	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7
TK6	5.8	5.9	5.9	6.6	6.6	5.8	5.8	5.8	5.9	5.8	5.8	5.8	5.8	5.8	5.8	6.0	6.0	6.0	6.1	5.8
TU1	4.9	4.9	4.9	4.8	4.8	4.9	4.8	4.8	4.8	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.8	4.8	4.8	4.9
TU2	2.6	2.6	2.6	2.5	2.5	2.6	2.5	2.5	2.3	2.6	2.6	2.6	2.6	2.6	2.6	2.6	2.5	2.5	2.4	2.6
WA1	6.8	6.4	6.4	7.0	7.0	6.8	6.8	6.8	6.4	6.8	6.8	6.8	6.8	6.8	6.8	7.3				6.8
WA2	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.1	7.0	7.0	7.0	7.0	7.0	7.0	7.0	6.9	7.0	7.0	7.0
WA3	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9
WA4	3.6	3.6	3.6	3.6	3.6	3.6	3.6	3.6	3.4	3.6	3.6	3.6	3.6	3.6	3.6	3.6	3.6	3.6	4.8	3.6
WA5	5.3	5.3	5.4	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.3	5.3
WA6	4.9	4.9	4.9	4.8	4.8	4.9	4.8	4.8	4.8	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.8	4.8	4.8	4.9
WA7	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.5	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4
WA8	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.1	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	4.6	3.0
WA9	1.4	1.4	1.4	1.4	1.3	1.4	1.3	1.3	1.3	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	2.2	1.4
WH1	5.7	5.7	5.7	5.7	5.6	5.7	5.7	5.6	5.6	5.7	5.7	5.7	5.7	5.7	5.6	5.7	5.6	5.6	5.6	5.7
WH2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.5	3.2
WN1	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.2	2.0	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3
WN2	7.9	7.9	7.9	7.9	7.9	7.9	7.9	8.0	8.0	7.9	7.9	7.9	7.9	7.9	7.9	7.9	7.8	7.8	7.8	7.9
WN3	2.7	2.7	2.7	2.7	2.7	2.7	2.7	2.6	2.3	2.7	2.7	2.7	2.7	2.7	2.7	2.7	2.8	2.7	2.7	2.7
WN4	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	5.0	4.8	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9
WN5	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.8	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.7	7.7	7.7	7.6

Table S2.2a: MCI and QMCI quality classes and average MCI scores of the taxa comprising the common and rare components in communities from 64 sites sampled for the National River Water Quality Network of New Zealand during the austral summer and autumn of 2005. Common and rare taxa defined based on the site-specific criteria presented in Table 2.1. NA values indicate samples were taxa belonged to the rare components under respective criteria.

	MCI class	QMCI class	Full	Singletons		Doubletons		5 indvs		10 indvs		0.1 %		0.5 %		1 %		5 %		Subs 200	
				Com	Rare	Com	Rare	Com	Rare	Com	Rare	Com	Rare	Com	Rare	Com	Rare	Com	Rare	Com	Rare
AX1	2	4	5.5	5.3	6.5	5.4	5.7	5.2	6.0	4.7	5.9	5.5	NA	5.4	5.7	5.2	6.0	4.7	5.9	5.5	5.5
AX2	3	1	5.2	5.7	4.7	6.0	4.8	8.0	4.6	8.0	4.6	5.2	4.8	5.7	4.8	6.0	4.8	8.0	4.6	5.2	5.8
AX3	1	1	6.8	7.7	6.0	7.0	6.8	8.0	6.6	NA	6.8	6.8	NA	6.8	NA	6.8	NA	6.8	NA	6.8	NA
AX4	4	4	4.4	4.3	5.0	3.8	5.3	4.0	4.6	4.0	4.6	4.4	NA	4.4	NA	4.4	NA	4.7	4.3	4.4	NA
CH1	2	3	5.8	5.4	6.6	5.4	6.4	5.8	5.7	5.6	5.9	5.8	NA	5.4	6.2	5.7	5.8	4.4	6.1	5.8	5.8
CH2	3	4	5.1	5.2	4.8	5.1	5.2	5.4	4.6	4.9	5.3	4.5	5.6	3.7	5.7	4.0	5.5	4.3	5.2	4.9	5.1
CH3	3	1	5.0	4.6	9.0	4.7	6.0	5.0	5.0	5.0	5.0	4.7	5.5	5.0	5.0	4.8	5.1	4.3	5.2	5.0	5.0
CH4	3	4	4.7	4.5	5.2	4.4	5.0	4.5	4.9	4.2	5.0	4.7	NA	4.5	5.2	4.4	5.0	4.2	5.0	4.7	4.6
DN1	3	2	5.1	5.1	5.5	5.1	5.5	5.5	4.3	5.0	5.2	5.1	6.3	5.0	5.4	5.0	5.4	6.0	5.1	5.1	5.1
DN2	3	1	5.4	5.5	4.3	5.7	4.3	5.4	5.4	5.6	5.3	5.6	4.9	5.8	5.2	6.2	5.0	6.8	5.1	4.7	5.5
DN3	3	3	4.9	4.8	5.0	4.8	5.2	4.6	5.2	4.0	5.4	4.8	5.3	4.6	5.3	3.8	5.5	5.0	4.8	5.5	4.5
DN5	4	2	4.4	4.3	7.0	4.2	6.0	3.5	6.2	3.5	6.2	4.2	6.0	3.9	5.0	4.4	4.4	4.7	4.4	4.9	4.2
DN6	2	2	6.0	6.1	5.8	6.1	5.8	6.2	5.7	6.0	6.0	6.1	5.8	6.0	6.0	6.0	6.0	5.8	6.0	4.4	6.1
DN7	2	2	5.7	5.9	5.0	6.1	4.9	5.7	5.7	5.3	5.9	5.9	5.0	5.3	5.9	5.4	5.8	4.8	5.9	6.0	5.7
DN8	3	2	5.4	5.2	6.0	4.8	6.3	4.4	6.1	4.4	6.1	4.3	5.7	4.8	5.7	5.0	5.6	7.0	5.3	5.9	4.9
DN9	3	3	4.8	4.6	5.0	4.7	4.9	4.1	5.3	4.1	5.3	4.8	NA	4.6	4.9	4.1	5.3	5.7	4.6	5.3	4.7
DN10	3	4	4.7	4.1	6.3	4.1	5.3	4.3	5.0	4.8	4.6	4.7	NA	4.1	6.3	4.1	5.3	4.6	4.7	4.8	4.9
GS2	2	2	6.3	6.3	6.5	6.4	5.3	7.1	4.3	7.1	5.7	6.3	6.5	7.1	4.3	7.1	5.7	6.0	6.4	6.3	6.3
GS3	2	1	6.1	6.7	4.4	6.5	5.2	6.4	5.8	6.6	5.8	6.7	4.4	6.4	5.8	6.6	5.8	5.7	6.1	6.1	6.1
GS4	3	2	5.0	5.0	NA	4.3	8.0	4.3	8.0	5.0	5.0	5.0	NA	5.0	NA	5.0	NA	4.3	8.0	5.0	NA
GY2	2	4	6.3	6.1	7.0	5.9	7.0	5.9	6.7	5.3	7.1	6.3	NA	5.9	7.0	5.9	6.7	5.2	6.8	6.3	6.3
GY3	2	4	6.2	6.3	5.7	6.3	5.7	6.4	5.8	5.8	6.7	6.3	5.7	6.4	5.8	5.8	6.7	5.0	6.4	6.2	6.2
GY4	1	2	6.9	6.9	NA	6.3	8.5	6.4	7.7	5.3	7.8	6.9	NA	6.3	8.5	6.4	7.7	5.3	7.8	6.9	6.9
HM1	2	3	5.6	5.4	7.5	5.4	6.7	5.4	6.0	5.3	6.1	5.6	NA	5.4	6.0	5.3	6.1	4.4	6.1	5.6	5.6
HM3	4	4	3.9	3.5	6.0	3.3	4.7	3.3	4.7	3.7	4.0	3.9	4.0	3.5	5.0	3.3	4.5	3.7	4.0	3.9	3.9
HM6	4	4	4.1	4.1	3.5	3.6	4.7	4.1	4.0	3.8	4.2	4.1	NA	3.9	4.3	4.1	4.0	4.0	4.1	4.1	4.1
HV1	1	1	7.3	6.9	9.0	6.7	9.0	6.6	8.2	6.8	7.7	6.9	9.0	6.6	8.2	6.8	7.7	7.3	7.2	7.3	7.3
HV2	3	1	5.1	5.3	4.0	5.3	4.0	5.6	3.7	5.5	4.3	5.3	3.7	5.5	4.3	5.0	5.2	6.0	4.9	5.1	5.1
HV3	3	3	5.2	5.1	5.3	5.1	5.3	5.1	5.3	5.4	4.8	5.2	5.7	5.1	5.5	5.1	5.5	5.0	5.1	5.2	5.2
HV4	1	1	7.8	7.7	8.0	8.2	7.4	7.8	7.9	7.8	7.9	7.8	NA	7.8	7.9	7.8	7.9	7.0	8.0	7.8	7.8
HV6	2	2	5.9	6.3	4.0	6.3	4.0	5.8	6.2	5.3	6.6	5.9	NA	6.3	4.0	5.8	6.2	4.8	6.4	5.9	5.9
NN1	2	3	6.4	6.2	7.5	5.9	7.6	6.5	6.1	6.3	6.4	6.2	7.0	6.3	6.3	5.9	6.6	6.0	6.4	6.4	6.4
NN2	2	1	6.3	6.3	6.0	6.3	6.0	8.2	5.4	8.0	5.8	6.3	NA	6.3	NA	6.3	6.0	8.2	5.4	6.3	NA
NN3	2	1	6.2	6.6	5.3	7.1	5.4	7.1	5.5	7.3	5.7	6.2	NA	7.1	5.4	7.1	5.5	7.3	6.0	6.2	6.2
NN4	2	1	5.7	5.8	5.5	5.7	5.7	5.7	5.7	6.2	5.0	5.8	5.7	6.2	5.2	6.8	5.1	7.0	5.4	5.7	5.7
NN5	2	2	6.0	5.9	6.7	5.4	7.6	4.9	7.2	5.3	6.5	6.0	5.6	5.5	5.7	5.3	6.2	6.0	6.0	6.0	6.0
RO1	2	1	5.7	5.9	5.3	6.0	5.4	6.6	5.2	6.5	5.3	5.9	5.3	6.6	5.2	6.5	5.3	7.3	5.4	5.7	5.7
RO3	3	1	5.3	6.3	3.6	6.6	4.2	7.2	4.4	8.0	4.6	5.3	NA	5.3	NA	6.3	3.6	7.4	4.5	5.3	NA
RO4	1	3	6.8	7.0	6.0	6.9	6.5	6.7	6.9	6.8	6.7	6.9	6.5	6.4	7.0	7.0	6.7	6.0	6.8	6.9	6.8
RO5	4	4	2.7	2.0	3.3	2.5	2.8	2.5	2.8	3.0	2.7	2.7	NA	2.7	NA	2.7	NA	2.0	3.3	2.7	NA
TK1	2	1	6.4	6.4	6.0	6.4	6.0	6.7	5.7	6.3	6.5	6.4	6.0	6.3	6.5	6.4	6.4	7.0	6.3	6.4	6.4
TK2	3	3	4.9	5.1	3.0	5.6	3.0	6.2	3.4	6.4	3.7	4.9	NA	5.7	3.5	6.4	3.7	5.8	4.4	4.9	4.9
TK3	3	3	5.0	4.8	6.0	5.4	4.0	5.6	4.0	5.3	4.7	5.0	NA	4.8	6.0	5.4	4.0	5.3	4.7	5.0	5.0
TK4	3	1	5.4	4.8	6.3	5.3	5.4	5.3	5.4	6.0	5.2	5.4	NA	5.4	NA	4.8	6.3	6.0	5.2	5.4	NA
TK5	2	1	6.4	6.4	NA	6.4	NA	6.7	5.5	6.0	6.8	6.4	NA	6.7	5.5	6.0	6.8	6.0	6.5	6.4	6.4
TK6	3	2	4.9	4.7	5.2	4.6	5.1	7.0	4.5	7.0	4.5	4.9	6.0	4.9	6.0	4.9	6.0	4.6	5.3	4.9	NA
TU1	2	3	6.0	6.4	4.3	6.2	5.2	5.8	6.3	5.2	6.5	6.1	5.8	5.1	6.5	4.7	6.5	4.6	6.4	6.0	6.0
TU2	2	4	5.8	5.0	7.2	4.6	7.0	4.7	6.7	4.4	6.5	4.6	7.0	4.4	6.5	4.4	6.5	2.5	6.3	6.1	5.8
WA1	1	1	7.6	6.0	8.7	6.0	8.7	7.0	7.8	7.0	7.8	7.6	NA	7.6	NA	7.6	NA	6.0	8.7	7.6	NA
WA2	1	1	6.6	6.6	6.4	6.6	6.6	5.8	7.2	5.4	7.1	6.6	NA	6.1	7.2	5.4	7.1	5.8	6.8	6.6	6.6
WA3	3	3	4.7	4.9	3.0	4.8	4.5	4.6	4.9	4.9	4.5	4.9	4.5	5.4	4.5	5.4	4.5	5.4	4.5	4.4	4.7
WA4	3	4	5.1	4.9	5.6	4.9	5.3	4.6	5.4	4.7	5.3	4.9	5.6	4.7	5.3	4.7	5.3	4.3	5.2	5.1	5.1
WA5	3	3	5.1	4.7	5.8	5.4	4.9	4.8	5.3	4.8	5.3	5.1	NA	4.7	5.8	4.9	5.3	4.6	5.4	5.1	5.1
WA6	2	3	6.2	6.4	4.5	6.2	6.0	5.8	6.9	5.2	7.0	6.1	6.8	5.1	6.9	4.7	6.9	4.6	6.7	6.3	6.2
WA7	3	3	5.1	5.5	4.0	5.6	4.3	5.7	4.5	5.6	4.8	5.6	4.8	5.6	5.0	5.0	5.2	5.5	5.1	5.4	5.1
WA8	3	4	4.8	4.6	6.0	3.9	6.1	4.0	5.6	3.6	5.6	4.6	6.0	4.0	5.6	4.0	5.2	4.0	5.1	4.8	4.8
WA9	4	4	3.8	3.8	NA	4.1	2.5	3.4	4.3	2.6	4.6	3.8	NA	2.7	4.9	1.5	4.3	1.5	4.3	3.8	3.8
WH1	3	2	5.4	5.6	4.3	5.9	3.8	5.5	5.3	5.0	5.5	5.4	6.0	5.6	4.8	5.0	5.7	5.0	5.5	5.4	5.4
WH2	4	4	4.4	4.3	4.5	3.8	5.4	3.3	5.4	3.3	5.1	4.4	NA	3.3	5.4	3.1	5.4	3.3	4.5	4.4	4.4
WN1	3	4	5.0	5.2	4.5	4.4	5.7	3.6	6.1	4.8	5.1	5.2	5.9	3.6	6.3	4.3	5.4	2.0	5.2	5.0	5.0
WN2	1	1	6.7	6.6	7.0	7.1	6.3	7.0	6.6	7.1	6.6	6.6	7.0	6.8	6.7	7.4	6.6	8.0	6.7	6.6	6.7
WN3	3	4	4.6	4.3	6.0	4.5	5.0	4.2	5.0	4.4	4.8	4.6	5.0	4.4	4.8	4.0	4.9	3.0	5.1	4.6	4.6
WN4	3	3	5.3	5.1	5.9	4.7	6.2	4.8	5.8	4.9	5.7	5.1	5.3	4.8	5.5	5.2	5.1	5.3	5.3	5.3	5.3
WN5	2	1	5.9	5.7	6.8	5.8	6.4	5.8	6.0	6.3	5.7	5.8	6.4	6.3	5.7	5.8	5.9	7.0	5.8	5.9	5.9

Table S2.2b: MCI and QMCI quality classes and average MCI scores of the taxa comprising the common and rare components in communities from 64 streams and rivers across New Zealand, during the austral summer and autumn of 2005. Common and rare taxa defined based on the study-wide criteria presented in Table 2.1. NA values indicate samples were taxa belonged to the rare components under respective criteria.

	MCI	QMCI	Uniq		Singleton		Doubleton		5 indvs		10 indvs		0.1 %		0.5 %		1 %		5 %		Low 25 %	
	class	class	Com	Rare	Com	Rare	Com	Rare	Com	Rare	Com	Rare	Com	Rare	Com	Rare	Com	Rare	Com	Rare	Com	Rare
AX1	2	4	5.5	NA	5.4	NA	4.4	NA	5.6	NA	4.5	NA	5.0	3.0	5.6	7.0	5.4	4.4	5.6	4.4	6.6	NA
AX2	3	1	5.1	NA	6.7	NA	4.4	NA	6.0	NA	5.0	5.0	4.8	6.0	5.5	5.0	5.7	5.5	5.3	2.5	5.8	NA
AX3	1	1	5.6	NA	5.9	NA	5.4	6.0	5.8	3.3	4.9	5.0	5.7	4.0	5.6	5.5	5.3	6.8	5.1	6.0	5.9	8.8
AX4	4	4	5.0	4.8	5.8	NA	4.9	NA	5.5	5.3	5.4	6.0	5.3	3.7	6.1	6.5	5.4	5.5	5.6	4.3	6.2	6.0
CH1	2	3	5.6	NA	5.4	NA	5.1	NA	5.4	NA	5.3	NA	5.5	5.5	5.5	5.9	5.5	5.1	5.5	4.9	6.0	NA
CH2	3	4	5.5	NA	5.7	NA	5.0	NA	5.7	NA	5.3	7.0	5.5	5.9	5.7	6.0	5.5	4.6	5.5	5.7	6.0	NA
CH3	3	1	6.1	NA	6.1	NA	5.2	NA	5.4	NA	5.3	NA	5.6	NA	5.9	5.2	5.2	8.0	5.5	5.3	6.4	NA
CH4	3	4	6.0	NA	5.8	NA	5.3	NA	5.4	6.3	5.1	7.7	5.3	5.6	5.6	6.0	5.5	6.6	5.5	5.8	6.3	5.5
DN1	3	2	6.0	5.2	5.8	NA	5.6	NA	5.7	5.5	5.6	5.0	5.4	6.4	5.6	5.4	5.6	5.8	5.5	4.9	6.3	5.8
DN2	3	1	5.8	5.1	5.5	6.1	5.4	4.9	5.6	6.3	5.5	5.7	5.5	5.9	5.5	5.6	5.5	5.0	5.5	5.2	5.8	4.8
DN3	3	3	5.5	NA	5.5	NA	5.2	NA	5.4	6.5	5.5	4.3	5.7	6.4	5.5	5.5	5.5	5.0	5.5	4.9	5.8	5.3
DN5	4	2	5.6	NA	5.6	NA	5.5	NA	5.5	NA	5.7	NA	5.7	6.7	5.7	6.4	5.5	6.2	5.5	4.9	6.5	NA
DN6	2	2	6.0	NA	5.6	NA	5.5	NA	5.4	4.0	5.3	3.3	5.6	5.7	5.5	5.9	5.5	5.3	5.5	5.2	6.0	4.8
DN7	2	2	6.2	NA	5.3	NA	5.2	NA	5.2	NA	5.7	NA	5.8	5.9	5.5	6.1	5.6	5.5	5.6	5.1	6.1	NA
DN8	3	2	5.9	NA	5.4	NA	4.9	NA	5.2	NA	5.5	NA	5.4	6.3	5.4	6.7	5.6	4.5	5.5	4.6	6.1	NA
DN9	3	3	5.5	6.0	5.9	4.8	5.1	4.3	5.6	6.6	5.6	3.8	5.5	6.1	5.6	5.7	5.6	4.9	5.5	5.4	5.7	6.0
DN10	3	4	5.1	NA	5.7	NA	4.8	NA	5.4	NA	5.3	NA	5.1	4.8	5.3	5.0	5.6	5.1	5.7	4.5	6.4	NA
GS2	2	2	5.4	NA	5.5	NA	5.6	6.0	5.8	3.3	5.4	5.0	5.6	5.5	5.7	6.1	5.6	5.2	5.4	5.3	6.1	8.8
GS3	2	1	5.8	NA	5.5	NA	5.5	NA	5.3	NA	5.4	NA	5.3	3.0	5.5	5.7	5.8	5.2	5.5	4.6	6.1	NA
GS4	3	2	5.2	NA	7.0	NA	5.7	NA	5.6	NA	5.0	NA	5.4	NA	5.5	3.0	5.7	6.0	5.3	2.0	5.3	NA
GY2	2	4	5.1	NA	6.1	NA	5.1	NA	5.4	NA	5.0	NA	5.5	6.6	5.7	6.1	5.6	4.8	5.4	4.9	5.8	NA
GY3	2	4	5.8	NA	5.1	NA	4.9	NA	4.9	NA	5.2	NA	5.3	8.0	5.9	6.0	5.3	5.3	5.5	4.4	6.0	NA
GY4	1	2	6.1	NA	4.9	NA	5.6	NA	4.6	NA	4.8	NA	5.5	3.0	6.6	4.8	5.4	5.6	5.7	3.4	6.1	NA
HM1	2	3	6.3	NA	5.6	NA	5.3	NA	5.9	NA	5.4	NA	5.6	6.3	5.5	5.9	5.5	5.4	5.5	5.3	6.4	NA
HM3	4	4	5.3	NA	6.1	NA	5.2	NA	4.7	NA	4.8	NA	5.5	NA	5.5	4.0	6.0	4.5	5.7	5.7	6.9	NA
HM6	4	4	5.5	5.7	5.5	NA	4.9	NA	5.3	7.8	4.9	4.0	4.8	4.1	5.4	5.8	5.7	5.5	5.7	4.7	6.1	6.5
HV1	1	1	5.8	6.0	4.9	NA	5.1	4.9	5.1	4.8	5.0	8.0	5.3	4.2	5.6	6.1	5.3	5.2	5.1	5.1	5.5	4.8
HV2	3	1	6.0	NA	5.8	NA	4.8	NA	5.2	NA	4.7	NA	4.9	5.8	5.6	6.0	5.5	5.2	5.5	4.6	6.1	NA
HV3	3	3	5.9	NA	6.3	NA	5.5	NA	6.1	NA	5.0	NA	5.0	NA	5.6	5.3	5.6	7.0	5.5	6.0	6.6	NA
HV4	1	1	6.4	NA	5.2	NA	5.7	NA	5.0	5.5	5.6	7.5	5.2	3.0	6.0	5.1	5.1	5.6	5.2	5.4	6.1	NA
HV6	2	2	5.9	5.0	5.7	NA	5.1	NA	5.3	3.8	5.5	5.3	5.2	4.0	5.7	5.8	5.6	4.7	5.4	3.8	5.7	4.8
NN1	2	3	5.8	NA	5.0	NA	5.0	NA	5.0	NA	4.9	4.3	5.5	4.2	5.5	6.3	5.2	4.3	5.4	4.6	5.7	NA
NN2	2	1	5.8	NA	5.8	NA	5.5	NA	5.0	NA	5.1	NA	5.5	6.7	5.8	4.9	5.5	6.0	5.6	5.2	6.2	NA
NN3	2	1	5.2	8.0	6.0	NA	5.7	NA	5.4	4.7	5.4	6.4	5.6	7.0	5.6	5.3	5.7	6.0	5.5	5.8	6.1	5.5
NN4	2	1	6.6	NA	5.2	NA	4.7	NA	5.0	4.0	5.2	3.3	5.4	2.3	5.6	5.8	5.2	4.0	5.3	3.8	5.4	4.8
NN5	2	2	6.2	NA	5.7	NA	5.4	NA	5.3	5.5	5.4	7.5	5.2	4.6	5.7	6.4	5.5	5.7	5.4	4.8	5.8	NA
RO1	2	1	5.3	NA	5.3	NA	5.1	NA	5.8	6.0	4.9	7.3	5.6	6.5	5.6	6.0	5.3	5.8	5.4	5.5	5.9	4.8
RO3	3	1	5.8	5.7	5.2	6.1	4.3	5.9	5.3	4.7	5.2	4.4	5.2	5.1	5.6	5.8	5.3	4.9	5.5	5.3	5.8	6.0
RO4	1	3	6.0	NA	5.0	NA	4.9	NA	5.1	NA	5.0	4.3	5.5	4.8	5.6	5.7	5.1	4.9	5.3	4.7	5.6	NA
RO5	4	4	4.8	NA	7.1	NA	6.0	NA	6.2	NA	6.0	NA	5.6	9.0	5.1	6.8	6.1	6.8	5.6	5.8	6.7	NA
TK1	2	1	6.2	NA	4.9	NA	4.7	NA	5.2	NA	4.7	NA	5.1	3.0	5.5	6.3	5.3	5.0	5.4	5.2	6.3	NA
TK2	3	3	5.8	NA	5.1	NA	4.7	NA	5.4	NA	4.7	NA	5.4	4.0	5.5	6.0	5.6	5.3	5.6	6.2	6.6	NA
TK3	3	3	5.5	NA	6.1	NA	5.4	NA	5.6	NA	5.0	NA	5.5	3.0	5.3	6.4	5.6	5.9	5.6	5.8	6.4	NA
TK4	3	1	5.5	NA	5.0	NA	4.3	NA	4.7	NA	4.7	NA	5.3	NA	5.4	5.3	5.4	3.3	5.6	3.0	6.2	NA
TK5	2	1	5.5	NA	5.1	NA	4.9	NA	5.7	NA	5.6	NA	5.8	NA	5.9	6.5	5.3	5.8	5.1	4.2	5.9	NA
TK6	3	2	5.0	NA	5.3	NA	6.2	NA	4.8	NA	4.9	4.3	5.3	5.0	6.0	4.9	5.8	5.6	5.7	4.6	5.9	NA
TU1	2	3	6.3	NA	4.9	NA	4.8	NA	5.2	NA	5.2	NA	5.4	5.0	5.6	6.5	5.4	5.1	5.5	4.5	6.2	NA
TU2	2	4	5.4	NA	6.0	NA	4.9	NA	5.8	NA	5.3	NA	5.6	6.2	5.7	6.1	5.4	5.5	5.3	5.1	6.3	NA
WA1	1	1	5.9	NA	6.0	NA	6.3	NA	6.7	NA	5.1	NA	6.5	5.5	NA	6.0	NA	5.4	NA	5.1	6.7	NA
WA2	1	1	5.6	NA	5.3	NA	4.7	NA	5.5	NA	5.3	NA	5.0	5.1	5.6	6.3	5.4	5.1	5.5	4.3	6.6	NA
WA3	3	3	5.8	NA	5.3	NA	4.8	NA	5.7	NA	5.7	5.0	5.3	5.8	5.6	6.5	5.5	5.3	5.5	4.5	6.3	NA
WA4	3	4	5.7	NA	4.8	NA	5.0	NA	5.5	NA	4.9	7.0	5.7	5.3	5.5	6.3	5.5	4.2	5.5	4.9	5.9	NA
WA5	3	3	5.7	4.9	5.4	5.3	5.4	5.4	5.4	8.8	5.7	6.0	5.4	7.6	5.6	5.3	5.7	5.7	5.5	4.6	6.1	5.0
WA6	2	3	6.1	NA	4.8	NA	4.7	NA	5.0	NA	5.1	NA	5.4	5.0	5.7	6.4	5.5	4.5	5.5	4.3	5.8	NA
WA7	3	3	5.7	NA	5.7	NA	5.4	6.1	5.2	5.3	5.6	5.0	5.5	6.6	5.4	5.9	5.6	5.0	5.5	5.5	5.9	6.8
WA8	3	4	4.8	5.4	5.3	5.4	4.7	7.4	5.7	3.8	5.3	4.8	5.7	4.4	5.5	5.7	5.5	5.0	5.5	4.6	6.1	4.5
WA9	4	4	5.3	4.5	6.4	NA	5.5	5.1	5.8	6.6	5.6	6.6	5.4	6.1	5.3	5.2	5.6	5.4	5.5	6.3	6.3	4.4
WH1	3	2	5.4	NA	5.2	NA	4.7	NA	5.3	NA	5.0	7.0	5.8	6.8	5.6	5.4	5.6	4.3	5.7	4.5	6.2	NA
WH2	4	4	5.4	NA	6.2	NA	5.1	NA	5.7	NA	5.7	NA	5.4	5.2	5.4	6.1	5.8	5.5	5.7	5.5	6.2	NA
WN1	3	4	5.9	NA	5.7	NA	5.4	NA	5.5	NA	5.9	NA	5.2	9.5	6.0	5.5	5.4	5.3	5.6	4.7	6.3	NA
WN2	1	1	5.5	NA	5.3	NA	5.2	NA	5.5	5.9	5.5	6.4	5.4	5.8	5.6	5.6	5.8	4.8	5.4	4.9	5.8	5.3
WN3	3	4	5.4	NA	5.5	NA	5.5	NA	5.3	NA	6.1	NA	6.0	6.0	5.5	5.7	5.8	6.2	5.5	4.9	6.2	NA
WN4	3	3	5.7	NA	5.7	NA	5.5	NA	5.3	NA	5.6	NA	5.7	7.0	5.5	5.7	5.5	5.5	5.5	5.5	6.3	NA
WN5	2	1	5.7	NA	5.8	NA	5.7	NA	5.0	5.5	5.7	7.5	5.8	5.3	5.8	6.2	5.4	5.8	5.4	5.4	6.5	NA

Appendix B – Supplementary material for Chapter 3

Table S3.1: Species collected with Kick-nets (K), Surber samplers (S), UV-light traps (L), SLAM traps (M) from 15 streams in the Tongariro National Park, New Zealand, March 2017. On the left table, the identification level of trap samples has been raised to that of benthic samples.

Benthic identification level	K	S	L	M
Aloecentrella sp.	+	+		
Aoteapsyche sp.	+	+	+	+
Beraeoptera roria	+	+	+	+
Confluens hamiltoni	+	+		+
Costachorema sp.	+	+		
Costachorema callistum	+	+	+	+
Costachorema hecton		+		
Costachorema psaropterum		+		
Costachorema xanthopterum	+	+	+	
Helicopsyche sp.	+	+	+	
Hydrobiosella mixta			+	
Hudsonema allienum	+			
Hudsonema amabile	+	+		
Hydrobiosidae	+	+		
Hydrobiosis sp.	+	+		
Hydrobiosis centralis/falcis	+	+	+	+
Hydrobiosis charadrea/clavigera/frater gr.		+	+	
Hydrobiosis charadrea	+	+	+	
Hydrobiosis copis	+			
Hydrobiosis frater		+		
Hydrobiosis gollanis	+			
Hydrobiosis parumbripennis	+	+	+	+
Hydrobiosis soror	+	+	+	+
Hydrobiosis styracine	+			
Hydrobiosis umbripennis gr.	+	+		+
Hydrochorema lyfordi		+		
Hydrochorema sp1	+	+		
Hydroptilidae		+		
Neurochorema sp.	+	+	+	+
Oecetis sp.	+			
Oeconesus maori	+	+	+	+
Oeconesus similis	+			
Olinga feredayi	+	+		
Orthopsyche fimbriata	+	+		
Orthopsyche thomasi	+			
Oxyethira sp.	+	+	+	+
Paroxyethira sp.	+		+	+
Philorheithrus sp.	+			
Plectrocnemia maclachlani			+	+
Polyplectropus sp.	+		+	+
Psilochorema sp.	+	+	+	+
Pycnocentria evecta	+	+		+
Pycnocentria funerea	+	+		+
Pycnocentria sp.	+	+	+	+
Pycnocentrodes sp.	+	+	+	+
Synchorema tillyardi				+
Tiphobiosis cataractae				+
Tiphobiosis cowiei			+	
Tiphobiosis veniflex			+	
Triplectides dolichos/obsoletus	+	+	+	
Triplectidina moselyi	+		+	
Zelolessica cheira	+	+	+	+

Adult identification level	L	M
Aoteapsyche catherinae	+	
Aoteapsyche colonica	+	+
Aoteapsyche tepoka	+	
Beraeoptera roria	+	+
Confluens hamiltoni		+
Costachorema callistum	+	+
Costachorema xanthopterum	+	
Helicopsyche albescens	+	
Hydrobiosella mixta	+	
Hydrobiosis centralis	+	
Hydrobiosis charadraea	+	
Hydrobiosis clavigera	+	
Hydrobiosis falcis	+	+
Hydrobiosis harpidiosa	+	
Hydrobiosis parumbripennis	+	+
Hydrobiosis soror	+	+
Hydrobiosis umbripennis		+
Neurochorema armstrongi	+	+
Neurochorema confusum	+	
Oeconesus maori	+	+
Oxyethira albiceps	+	+
Paroxyethira hendersoni	+	+
Paroxyethira hintoni		+
Paroxyethira teika		+
Plectrocnemia maclachlani	+	+
Polyplectropus altera	+	+
Polyplectropus aurifusca		+
Polyplectropus impluvii		+
Psilochorema donaldsoni	+	
Psilochorema leptoharpax	+	
Psilochorema macroharpax	+	
Psilochorema mimicum	+	+
Pycnocentria evecta		+
Pycnocentria funerea		+
Pycnocentria gunni	+	+
Pycnocentrodes aeris	+	+
Pycnocentrodes aureolus	+	+
Synchorema tillyardi		+
Tiphobiosis cataractae		+
Tiphobiosis cowiei	+	
Tiphobiosis veniflex	+	
Triplectides dolichos	+	
Triplectidina moselyi	+	
Zelolessica cheira	+	+

Table S3.2: Comparison of the number of shared taxa between pairs of sampling methods for the complete assemblage (Total) and their rare components (Rare) using Generalised Linear Models. Kick-nets (K), Surber samplers (S), UV-light traps (L) and SLAM, Sea-Land- Air-Malaise, traps (M). Benthic samples were collected in15 streams in the Tongariro National Park of New Zealand, UV-light trap samples in 14 streams and SLAM traps in 12 streams, March 2017.

	Total		Rare	
Method pairs	|z| value	Pr(>|z|)	|z| value	Pr(>|z|)
KL vs KS	-5.754	0.001***	-3.403	0.008**
KM vs KS	-3.948	0.0011**	-2.952	0.034*
SL vs KS	-4.1	0.001***	-3.308	0.011*
SM vs KS	-4.35	0.001***	-4.816	0.001***
LM vs KS	-4.526	0.001***	-4.057	0.001***
KM vs KL	-0.183	1.000	-1.099	0.872
SL vs KL	1.858	0.407	0.39	0.999
SM vs KL	0.242	1.000	-1.92	0.368
LM vs KL	-0.751	0.973	-1.224	0.812
SL vs KM	1.492	0.650	1.349	0.740
SM vs KM	0.356	0.999	-0.265	1.000
LM vs KM	-0.471	0.997	0.208	1.000
SM vs SL	-1.306	0.766	-2.332	0.167
LM vs SL	-2.066	0.286	-1.605	0.573
LM vs SM	-0.876	0.948	0.621	0.988

Table S3.3: Comparison of biodiversity metrics calculated from samples collected with four sampling methods, for the complete assemblage (Total) and their rare components (Rare) using Generalised Linear Mixed Models with method as a fixed effect and site as a random factor. Samples collected from 15 streams in the Tongariro National Park of New Zealand, March 2017.

		Total		Rare	
Methods	Biodiversity Metric†	z value	Pr(>|z|)	z value	Pr(>|z|)
Kick-Surber	NSp	**2.70**	**0.03***	**3.58**	**0.002****
	Chao1 NSp	0.68	0.90	0.94	0.79
	EfNSp	-1.21	0.62	1.65	0.35
	REv	-2.23	0.12		
	Rare species %	2.13	0.15		
	Chao1 Rare species %	1.42	0.49		
	Rare individuals %	0.43	0.97		
Kick-UV-light	NSp	-**3.86**	**<0.001*****	-2.54	0.05.
	Chao1 NSp	-1.70	0.32	-1.08	0.70
	EfNSp	-0.78	0.86	-**2.67**	**0.04***
	REv	1.63	0.36		
	Rare species %	2.05	0.17		
	Chao1 Rare species %	1.25	0.59		
	Rare individuals %	**3.14**	**0.008****		
Kick-SLAM	NSp	-**6.32**	**<0.001*****	-**5.51**	**<0.001*****
	Chao1 NSp	-2.47	0.07	-1.88	0.24
	EfNSp	-**4.14**	**<0.001*****	-**5.22**	**<0.001*****
	REv	1.44	0.48		
	Rare species %	1.23	0.61		
	Chao1 Rare species %	0.82	0.85		
	Rare individuals %	**2.78**	**<0.03***		
Surber-UV-light	NSp	-**6.33**	**<0.001*****	-**5.88**	**<0.001*****
	Chao1 NSp	-2.37	0.08.	-2.00	0.19
	EfNSp	0.41	0.98	-**4.29**	**<0.001*****
	REv	**3.81**	**<0.001*****		
	Rare species %	-0.03	1.00		
	Chao1 Rare species %	-0.14	1.00		
	Rare individuals %	2.72	**0.03***		
Surber-SLAM	NSp	-**8.33**	**<0.001*****	-**8.15**	**<0.001*****
	Chao1 NSp	-**3.11**	**0.01***	-**2.76**	**0.03***
	EfNSp	-**3.00**	**0.01***	-**6.77**	**<0.001*****
	REv	**3.47**	**0.003****		
	Rare species %	-0.76	0.87		
	Chao1 Rare species %	-0.52	0.96		
	Rare individuals %	2.367	0.08		
UV-light-SLAM	NSp	-**2.8**	**0.005****	-**3.14**	**0.002****
	Chao1 NSp	-1.52	0.13	-1.46	0.15
	EfNSp	-**4.126**	**<0.001*****	-**2.903**	**0.004****
	REv	-0.06	0.95		
	Rare species %	-0.32	0.75		
	Chao1 Rare species %	-0.05	0.96		
	Rare individuals %	-0.381	0.70		

† NSp = Number of species; Chao1 NSp = Chao1 species richness estimator; EfNSp = Effective number of species; REv = Relative evenness

Significance levels: * < 0.05, ** < 0.01, *** < 0.001

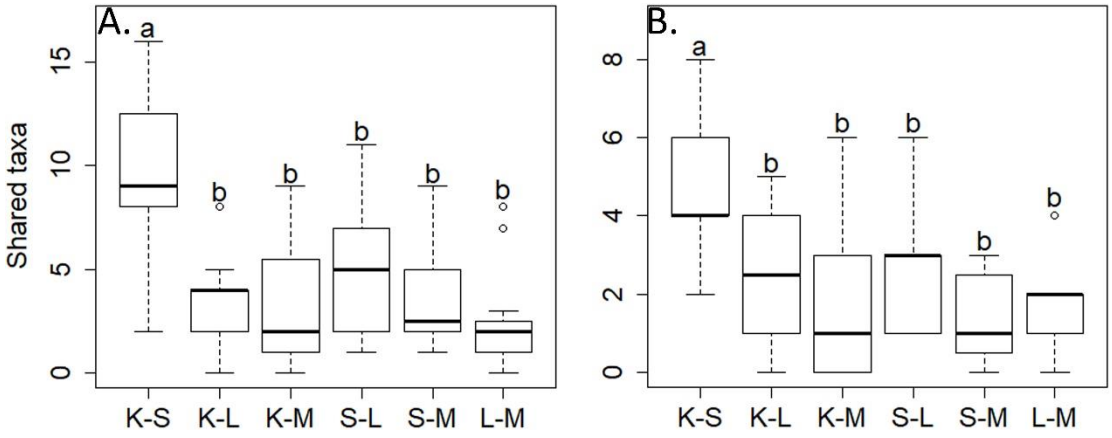

Figure S3.1: Number of shared taxa between the complete caddisfly assemblages (A) or their rare components (B), collected by each pair of sampling methods, kick-nets (K), Surber samplers (S), UV-light traps (L) and Sea-Land-Air-Malaise traps (M), in the Tongariro National Park, New Zealand, March 2017. Methods in the same plot sharing a letter did not differ ($P > 0.05$).

Appendix C – Supplementary material for Chapter 4

Table S4.1: Spearman's rank correlations among standardized environmental variables measured in 15 streams in the Tongariro National Park, New Zealand, March 2017. No significant correlations were found for any pair of variables.

rho	Depth	Velocity	CPOM	Slope	Water temperature	Conductivity	Filament cover	Mat cover	Biofilm cover	No periphyton	Embeddedness	Pfankuch index	Substrate size	Chlorophyll a	Altitude	Width	Canopy cover	Native forest	Native shrub	Planted forest	Bare ground	Undercut banks	Debris jams	Macrophyte abundance
Velocity	0.11																							
CPOM	0.04	-0.28																						
Slope	-0.17	0.29	-0.52																					
Water Temp	0.10	-0.03	0.05	-0.36																				
Conductivity	0.00	0.70	-0.41	0.16	-0.19																			
Filament cover	0.20	-0.03	-0.20	-0.28	-0.03	0.20																		
Algal mat cover	0.08	0.40	0.10	-0.10	0.09	0.50	-0.22																	
Biofilm cover	-0.24	-0.37	0.33	0.08	-0.06	-0.53	-0.58	-0.41																
No periphyton	0.47	-0.37	0.48	-0.35	-0.02	-0.47	0.20	-0.20	0.07															
Embeddedness	-0.01	0.08	-0.61	0.66	-0.45	0.20	-0.07	0.18	-0.18	-0.26														
Pfankuch index	0.29	0.22	0.07	-0.49	0.52	-0.07	0.18	-0.03	-0.30	0.19	-0.60													
Substrate size	0.49	0.14	-0.20	0.31	-0.04	0.07	-0.16	0.19	-0.36	-0.01	0.36	-0.01												
Chlorophyll a	-0.05	0.21	0.55	-0.19	-0.30	-0.10	-0.05	-0.01	0.30	0.04	-0.27	-0.11	-0.29											
Altitude	-0.42	0.26	-0.55	0.58	-0.50	0.59	-0.13	0.07	-0.05	-0.65	0.41	-0.45	0.11	-0.19										
Width	0.34	0.32	-0.26	0.11	0.36	0.41	-0.24	0.43	-0.26	-0.25	0.02	0.12	0.58	-0.47	0.26									
Canopy cover	0.04	-0.12	0.37	0.15	-0.09	-0.51	-0.49	-0.48	0.81	0.34	-0.22	-0.02	-0.10	0.29	-0.23	-0.25								
Native forest	-0.29	0.05	-0.30	0.57	-0.02	-0.08	-0.22	-0.45	0.41	-0.05	0.24	-0.35	0.04	-0.11	0.25	-0.07	0.52							
Native shrub	-0.04	-0.27	-0.12	-0.23	0.02	0.25	0.01	0.06	-0.14	-0.43	0.01	-0.07	0.14	-0.35	0.29	0.29	-0.40	-0.37						
Planted forest	0.27	-0.06	0.49	-0.48	0.00	-0.28	0.22	0.09	-0.05	0.42	-0.44	0.47	-0.35	0.47	-0.52	-0.43	0.02	-0.61	-0.32					
Bare ground	0.03	0.43	-0.03	0.20	0.13	0.23	-0.12	0.52	-0.40	-0.09	0.26	-0.09	0.39	-0.09	-0.03	0.47	-0.28	-0.10	-0.15	-0.32				
Undercut banks	-0.23	0.03	0.32	-0.23	0.22	-0.19	-0.26	0.43	0.08	0.30	-0.09	0.07	-0.25	0.06	-0.34	0.01	0.07	-0.08	-0.47	0.13	0.53			
Debris jams	-0.27	-0.32	0.43	0.13	0.02	-0.39	-0.36	-0.42	0.79	-0.03	-0.28	-0.28	-0.38	0.23	-0.08	-0.30	0.67	0.33	0.05	-0.06	-0.35	-0.16		
Macrophyte abundance	-0.16	0.05	-0.15	-0.01	-0.19	0.13	0.60	-0.21	-0.06	-0.13	0.16	-0.37	-0.42	0.45	0.04	-0.49	-0.24	0.13	-0.19	0.06	-0.15	-0.16	-0.02	
Moss abundance	0.34	-0.02	-0.22	0.51	-0.53	-0.03	0.07	-0.29	0.30	0.22	0.47	-0.50	0.19	0.12	0.22	-0.12	0.40	0.47	-0.35	-0.11	-0.25	-0.31	0.15	0.29

Appendix D – Supplementary material for Chapter 5

Table S5.1: Dispersal groups of macroinvertebrate taxa, based on body size, collected from three headwater streams and one mainstem site from each of three catchments, in and around the Tongariro National Park, New Zealand, February 2018.

		Dispersal groups			Network Position	
Order	Species	Passive Aquatic	Passive Terrestrial (<10mm)	Active Terrestrial (>10mm)	Headwaters	Mainstems
Ephemeroptera	*Ameletopsis perscitus*			+	+	
	Coloburiscus humeralis			+	+	+
	Ichthybotus hudsoni			+	+	
	Acanthophlebia cruentata			+	+	
	Austroclima jollyae		+		+	+
	Austroclima sepia		+		+	+
	Mauiulus sp		+		+	+
	Mauiulus luma		+			+
	Deleatidium sp			+	+	+
	Deleatidium lilii gr		+		+	+
	Deleatidium myzobranchia gr			+	+	+
	Deleatidium myzobranchia			+	+	+
	Neozephlebia scita		+		+	+
	Zephlebia sp		+		+	+
	Zephlebia dentata gr		+		+	+
	Zephlebia spectabilis		+		+	
	Zephlebia tuberculata		+			+
	Zephlebia versicolor		+			+
	Nesameletus sp			+	+	+
	Nesameletus ornatus			+	+	+
	Oniscigaster wakefieldi			+	+	
Plecoptera	*Austroperla cyrene*			+	+	+
	Stenoperla prasina			+	+	+
	Megaleptoperla grandis			+	+	
	Taraperla pseudocyrene			+	+	
	Zelandobius confusus gr		+		+	+
	Zelandoperla agnetis			+	+	
	Zelandoperla decorata			+	+	+
	Zelandoperla fenestrata			+	+	+
Trichoptera	*Conoesucidae sp*		+		+	+
	Beraeoptera roria		+		+	+
	Confluens hamiltoni		+		+	+
	Olinga sp		+		+	+
	Pycnocentria sp		+		+	+
	Pycnocentria evecta		+		+	+
	Pycnocentria funerea		+		+	+
	Pycnocentrodes sp		+		+	+
	Zelolessica cheira		+		+	
	Helicopsyche sp		+		+	
	Hydrobiosidae sp			+	+	+
	Costachorema sp			+	+	+
	Costachorema callistum			+	+	
	Costachorema hecton			+	+	
	Costachorema psaropterum			+	+	
	Costachorema xanthopterum			+		+
	Hydrobiosis sp			+	+	+
	Hydrobiosis charadrea/clavigera/falcis gr			+	+	+
	Hydrobiosis charadrea			+	+	
	Hydrobiosis copis			+	+	+
	Hydrobiosis falcis			+		+
	Hydrobiosis frater			+	+	
	Hydrobiosis harpidiosa			+	+	
	Hydrobiosis parumbripennis			+	+	+

Table S5.1: Continued…

Order	Species	Dispersal groups			Network positions	
		Passive Aquatic	Passive Terrestrial	Active Terrestrial	Headwaters	Mainstems
	Hydrobiosis soror			+	+	+
	Hydrobiosis styracine			+	+	
	Hydrobiosis umbripennis gr			+	+	+
	Hydrochorema sp			+	+	
	Neurochorema sp			+	+	+
	Neurochorema armstrongi			+	+	+
	Psilochorema sp			+	+	+
	Hydropsychidae sp			+	+	+
	Aoteapsyche sp			+	+	+
	Orthopsyche sp			+	+	
	Orthopsyche fimbriata			+	+	
	Orthopsyche thomasi			+	+	
	Oxyethira sp		+			+
	Hudsonema alienum			+	+	
	Hudsonema amabile			+		+
	Triplectides dolichos/obsoletus			+	+	
	Oeconesus sp			+	+	
	Hydrobiosella mixta			+	+	
Coleoptera	*Chrysomelidae sp*		+		+	
	Elmidae sp1		+		+	+
	Elmidae sp2		+		+	
	Hydraenidae sp		+		+	
	Orchmnt		+		+	
	Podaena sp1		+		+	
	Podaena sp2		+		+	
	Berosus sp		+			+
	Ptilodactylidae sp			+	+	
	Scirtidae sp1		+		+	
	Scirtidae sp2		+		+	
	Staphylinidae sp			+	+	+
Diptera	*Neocurupira hudsoni gr*		+		+	
	Ceratopogoninae		+		+	
	Harrisius		+			+
	Maoridiamesa		+		+	+
	Orthocladiinae A		+		+	+
	Orthocladiinae B		+		+	+
	Orthocladiinae C		+		+	+
	Orthocladiinae D		+		+	+
	Orthocladiinae E		+		+	+
	Orthocladiinae F		+		+	+
	Orthocladiinae G		+			+
	Polypedilum		+		+	+
	Stictocladius		+		+	
	Tanypodinae A		+		+	+
	Tanypodinae B		+		+	
	Tanytarsini		+		+	+
	Paradixa sp		+		+	
	Empididae A		+		+	+
	Empididae B		+		+	
	Muscidae sp			+	+	
	Austrosimulium australense gr		+		+	+
	Tabanidae sp			+	+	
	Mischoderus sp			+	+	+
	Aphrophila sp			+	+	+
	Eriopterini sp			+	+	+
	Molophilus sp		+		+	
Other	*Archichauliodes diversus*			+	+	+
	Collembola	+			+	+
	Cura sp	+			+	+
	Gyraulus sp	+			+	
	Hydracarina	+			+	+
	Mesoveliidae sp		+		+	+
	Oligochaeta	+			+	+
	Potamopyrgous antipodarum	+			+	+

Table S5.2: Pairwise PERMANOVA with 9999 permutations, comparing macroinvertebrate assemblages collected in February 2018 from three river basins in and around the Tongariro National Park, New Zealand, three headwater streams and one mainstem site from each basin, their common and rare components and the differently dispersing groups within each assemblage, passively drifting aquatic dispersers (PaAq), taxa with passively dispersing terrestrial adults (PaTe) and taxa with actively dispersing terrestrial adults (AcTe).

Assemblage		All	PaAq	PaTe	AcTe
		F			
Total	Network Position	**2.54***	0.07	2.3	**2.95***
	Basin	1.51	**0.52****	1.17	1.46
	Network Position : Basin	1.03	0.09	1.09	1.14
Common	Network Position	2.42	-	**3.05***	**4.24****
	Basin	1.54	-	1.15	1.95
	Network Position : Basin	0.92	-	1.28	0.73
Rare	Network Position	1.24	0.06	1.21	1.38
	Basin	1.15	**0.46****	1.18	0.90
	Network Position : Basin	1.20	0.12	1.10	1.29

Significance levels: * < 0.05, ** < 0.01, *** < 0.001

Appendix E – DRC16 Statements of Contributions for Chapters 2 to 5

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STATEMENT OF CONTRIBUTION
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We, the candidate and the candidate's Primary 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:	Dimitrios Rados
Name/title of Primary Supervisor:	Professor Russell Death
In which chapter is the manuscript /published work:	Two

Please select one of the following three options:

○ The manuscript/published work is published or in press

- Please provide the full reference of the Research Output:

○ The manuscript is currently under review for publication – please indicate:

- The name of the journal:

- The percentage of the manuscript/published work that was contributed by the candidate: 90.00

- Describe the contribution that the candidate has made to the manuscript/published work:

Dimitrios Rados developed the hypothesis, reviewed literature, carried out the analysis, interpreted the data and wrote the manuscript. Professor Russell Death provided guidance on conception, methodology, manuscript development and editing.

◉ It is intended that the manuscript will be published, but it has not yet been submitted to a journal

Candidate's Signature:	Dimitrios Rados Digitally signed by Dimitrios Rados Date: 2021.09.07 17:28:38 +12'00'
Date:	07-Sep-2021
Primary Supervisor's Signature:	Russell Death Digitally signed by Russell Death Date: 2021.09.08 11:54:06 +12'00'
Date:	8-Sep-2021

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Name of candidate:	Dimitrios Rados
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In which chapter is the manuscript /published work:	Three

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○ The manuscript is currently under review for publication – please indicate:

- The name of the journal:

- The percentage of the manuscript/published work that was contributed by the candidate: 90.00

- Describe the contribution that the candidate has made to the manuscript/published work:

Dimitrios Rados developed the hypothesis, reviewed literature, carried out fieldwork, lab-work and the analysis, interpreted the data and wrote the manuscript. Professor Russell Death provided guidance on conception, methodology, manuscript development and editing. Dr. Ian Henderson provided guidance on macroinvertebrate identification, statistical analysis and manuscript development.

◉ It is intended that the manuscript will be published, but it has not yet been submitted to a journal

Candidate's Signature:	Dimitrios Rados Digitally signed by Dimitrios Rados Date: 2021.09.07 17:36:05 +12'00'
Date:	07-Sep-2021
Primary Supervisor's Signature:	Russell Death Digitally signed by Russell Death Date: 2021.09.08 11:54:46 +12'00'
Date:	8-Sep-2021

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Name of candidate:	Dimitrios Rados
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In which chapter is the manuscript /published work:	Four

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Dimitrios Rados developed the hypothesis, reviewed literature, carried out fieldwork, lab-work and the analysis, interpreted the data and wrote the manuscript. Professor Russell Death provided guidance on conception, methodology, manuscript development and editing. Dr. Ian Henderson provided guidance on macroinvertebrate identification, statistical analysis and results interpretation.

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STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the candidate and the candidate's Primary 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*.

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