Left in the Dark

The effect of agriculture on cave streams

Mahue i roto i te pō

Ko te ariā o te ahuwhenua i ngā hikuawa o ngā ana

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General Abstract

The ecology of cave stream environments has received far less attention than surface streams in New Zealand. As a result, the impacts of human stressors on the communities of caves are uncertain. The impacts of agricultural practices on surface stream communities are wide spread and well-studied. In the surface environment, agricultural use of the surrounding catchment has been associated with lower QMCI and EPT scores and influences the structuring of communities and trophic base. Given the knowledge that the effects found on the surface are so far reaching, the aim of this thesis was to establish the effect of agricultural land use on cave stream communities in comparison to surface stream communities, find principal stressors to the cave communities and to examine how land use practices alter the trophic bases of underground communities. The relationships between land use and cave stream communities were examined for four cave streams and their surface stream origins in the Manawatū region of New Zealand. The communities were sampled and in stream environmental measurements were taken. Catchment and riparian zones were mapped using GIS software to establish the extent of agricultural use of land. Stable isotope ratios of carbon and nitrogen were analysed for the communities at each site and for a few potential food sources to determine the source of energy for the communities. Cave stream communities were found to be influenced by surface land management practices. For both the cave and the surface environments, a negative relationship was found for QMCI and EPT against agricultural development. When cave and surface streams are considered apart, the relationship between QMCI and EPT with agriculture was not as steep. This was attributed to the attenuation of sediment transport through caves and the lack of photosynthetic ability limiting the negative impacts of nutrient sequestration. Although sediment attenuated through the cave, it was the primary stressor on stream communities both on the surface and within the caves. Between cave and surface environments within the same dominant catchment cover type, resource use was similar. Between catchment types, however, the use of resources was different with an increased reliance on biofilm derived energy in agricultural catchments for both cave and surface sites. Considered along with the change in functional feeding groups that was detected, it is likely that the changes in resource use by communities as a response to the different inputs from agriculture are reflected in a different community structure. Overall agriculture was found to have a definite impact on cave stream communities. It is likely that through sedimentation and changing resource uses, the communities are altered in a

way similar to what is found on the surface but to a lesser degree, reflecting the lower range of potential stressors on the cave from agriculture.

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Tēnei au, tēnei au
Te hōkai nei i tāku tapuwae
Ko te hōkai-nuku
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A Tāne-nui-a-rangi
I pikitia ai
Ki te Rangi-tūhāhā
Ki Tihi-o-Manono
I rokohina atu rā
Ko Io-Matua-Kore anake
I riro iho ai
Ngā Kete o te Wānanga
ko te Kete Tuauri
ko te Kete Tuatea
ko te Kete Aronui
Ka tiritiria, ka poupoua
Ki a Papatūānuku
Ka puta te Ira-tangata
Ki te whai-ao
Ki te Ao-marama

Tihei mauri ora!

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Two rock types in Piripiri cave

Introduction

The landscape of New Zealand has been extensively modified since the arrival of humans to the archipelago (McGlone, 1989). Beginning with Polynesian explorers and settlers, and continued by Europeans, the once extensively forested islands were quickly transformed into what we see today. The most striking and ubiquitous change experienced by all regions has been the conversion of the forested landscape into agricultural land. Just over half (51%) of the land area of New Zealand is covered in grassland making it the most common use of land (MFE, 2010). Unsurprisingly, human impact has had profound effects on the New Zealand biota. Many forest species are now extinct or have been extirpated from the mainland, restricted now to offshore islands, and others often only survive due to continuous conservation actions and the presence of "mainland islands". Many aquatic systems in New Zealand have also borne the brunt of human development. Today 74% of native freshwater fish species are classified as Threatened or At Risk (Allibone *et al.*, 2010). Many of these species have been shown to be negatively affected by the changing land use patterns (Hanchet, 1990; Joy, 2009; Allibone *et al.*, 2010). The invertebrate fauna of New Zealand streams has not been spared. As the proportion of pasture in a catchment increases, the communities often change and abundances of pollution tolerant taxa increase while pollution sensitive taxa are frequently absent (Quinn and Hickey, 1990; Scott *et al.*, 1994; Quinn *et al.*, 1997). The shift in land use threatens biodiversity and the ecology of many different environments. In recent years, with increasing attention to environmental issues, the impacts of this process have resulted in more research on land use riverine interactions (e.g. Doledec *et al.* (2011); Shilla and Shilla (2011)). However, this research has largely neglected the assessment of impacts on the subterranean environment.

Cave structure

The subterranean environment encompasses a large range of habitat types, both aquatic and terrestrial, from large underground rivers and caverns to tiny cracks in the rock (Romero, 2009). Caves are formed from lava flows, underground lakes and rivers, and dissolution. The most common caves are those formed by dissolution of limestone (Romero, 2009). A landscape that is structured by dissolution processes rather than by erosion is termed karst, and caves within these environments comprise a large portion of caves in the world (Culver and Pipan, 2009). These environments cover approximately 15% of the Earth's surface and with the right hydrological conditions allow for the creation of extensive cave networks. Most of these caves are formed in limestone (mostly formed of calcite, $CaCO_3$), which dissolves easily in the presence of an acid (Culver and Pipan, 2009):

$$CaCO_3 + H^+ \leftrightarrow Ca^{2+} + HCO_3^-$$
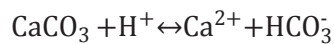
Acids suitable for the dissolution of calcite are often formed in rain and within soils (Williams, 1992). These waters enter the subterranean environment through the epikarst, the uppermost layer of rock. This environment consists of numerous cracks and pockets in the rock and forms an aquifer near to the surface. The percolation of water from this to the unsaturated zone beneath it can create fissures in the rock which expand and form networks of passages over tens of thousands to millions of years (Culver and Pipan, 2009). Caves formed from surface derived water, either percolating or entering as streams, are termed epigenic (Palmer, 1991). Alternatively, the water contained within the phreatic aquifer can interact with the percolating water and, following the relative lowering of the water table, create a hypogenic cave (Ford and Ewers, 1978; Palmer, 1991; Culver and Pipan, 2009). It is through these processes that many of the caves of the world are formed.

One example of the extent to which karst caves can reach is the 590 kilometres of passage of the Mammoth cave system in Kentucky, USA; a cave within a system of hundreds of caves. This cave hosts upwards of 200 species, twenty two percent of which are cave adapted, indicating the value of these environments for supporting biodiversity and as interesting ecological models (Barr, 1968).

Subterranean aquatic habitats have three important components: percolation, streams and resurgences (Culver and Pipan, 2009). Percolation of water from epikarst is responsible for the maintenance of flow within cave streams that do not originate as surface streams (Culver and Pipan, 2009). Beneath this, one finds the vadose (unsaturated) zone. The boundary zone of this area with the one beneath it, the phreatic zone, is where the majority of cave streams are found (Culver and Pipan, 2009). It is in this environment that this research focusses.

Cave Biology and Ecology

The cave world is dark (Culver and Pipan, 2009; Romero, 2009). Of all the differences between surface and cave streams this is the most obvious, with profound effects on the structuring and functioning of the ecological systems in the cave (Culver and Pipan, 2009). Lack of light affects primary production, behaviour, community structure and evolution (Culver and Pipan, 2009).

The lack of light in cave environments means that the most common method of primary production in terrestrial environments, photosynthesis, cannot occur. Thus, the character of nutrient sequestration and energy flow within caves is distinct from that on the surface. This has led to hypotheses of nutrient and energy limitation as major factors influencing the ecology of cave communities (Simon and Benfield, 2002; Datry *et al.*, 2005; Wood *et al.*, 2008; Huntsman *et al.*, 2011). For instance, Simon and Benfield (2002) found through

ammonium releases in cave streams and investigation of turnover of standing stocks of benthic organic carbon that cave streams were carbon limited but not nutrient limited. More evidence in support of carbon limitation in cave streams came with the investigation by Datry *et al.* (2005) of groundwater recharge rates. They found increasing dissolved organic carbon content increased diversity and abundance of aquifer invertebrates. Furthermore, Cooney and Simon (2009) found bottom-up control of carbon on microbial biomass but no effect of nutrients (N and P). In contrast, Simon and Benfield (2001) examined the breakdown of coarse particulate organic matter (CPOM) in cave streams and found no evidence of carbon limitation, suggesting that limitation may not be a ubiquitous feature of subterranean ecology. The weight of evidence however, suggests that many cave stream ecosystems are carbon, but not nutrient, limited.

However, while the lack of light makes photosynthesis impossible, there are caves which do host primary producers. First discovered in Romania, primary production without photosynthesis has been found to occur in Movile cave through chemolithotrophy (Chen *et al.*, 2009). Data suggest that this cave is fuelled through sulphur oxidation and ammonia and nitrate-oxidation (Chen *et al.*, 2009). These caves are thought to be much rarer and often to have no human accessible links to the surface, making discovery and study difficult. As a result of the rarity of this type of production and the lack of photosynthesis, most cave systems are dependent on surface derived sources for energy and nutrients.

Regardless of the degree of carbon or nutrient limitation, and notwithstanding the few chemolithotrophic exceptions, the main source of energy for cave fauna derives from the surface. There are a range of processes through which this energy enters into the system. The percolation of water into caves through the limestone brings with it dissolved organic matter (DOM) as well as minute invertebrates and microbial fauna. In some caves this input is the only input of material into the system (Simon *et al.*, 2003). Through this infiltration,

the water table and subterranean streams can maintain flow rates as well as receiving an input of organic matter. Flowing water brings with it these same inputs alongside much larger coarse (CPOM) and fine particulate organic matter (FPOM) (Culver and Pipan, 2009). The movement of animals is also an important factor in the energetic environment of cave systems. In some caves the influx of animals to the cave in the form of both bats and of non-cave dwelling animals accidentally getting trapped within contributes greatly to the overall energy in the environment as well as structuring the community within (Schneider *et al.*, 2011).

Cave stream communities are not only reliant on the surface for an input of energy, but in many cases also for an input of colonists. That is, the communities found in caves are often depauperate and consist mainly of a subset of the surface fauna, reflecting the dependency of the subterranean environment on surface derived inputs (Gibert and Deharveng, 2002; Watson, 2010). Certain feeding groups appear less frequently in cave systems suggesting that this aspect of life history is important in structuring cave communities (Gibert and Deharveng, 2002). Additionally, drift densities of species in surface communities are, in many cases, related to the cave densities suggesting a role for colonisation rates in structuring communities (Watson, 2010). The input drifting from the surface is unlikely to be the only structuring agent considering the evidence for energy limitation and differences in benthic and drift densities that has been observed (Simon and Benfield, 2001; Watson, 2010). Thus, it is likely that communities within caves are structured by some combination of drift, behavioural preference and ability to obtain resources competitively in the harsh environment.

 Whatever the source of energy for the cave fauna, there are sound reasons *a priori* to assume that one can expect a difference in community composition underground when compared with the surface. For instance, it is unlikely to expect algal or macrophyte grazers

to be common. The unique demands of life in the darkness and the potential paucity of resources available has led to unique evolutionary responses that affect the ecology of many of the animals that call caves home. These responses manifest behaviourally, morphologically and physiologically enabling increased fitness underground (Poulson, 1963; Jones and Culver, 1989). There are also responses, however, that are not related to fitness and that convey no apparent benefit. The so called troglomorphic features, such as blindness or a lack of eyes, depigmentation and increased chemo- and mechanoreceptors, among others, have captivated researchers of the hypogea for years. Some observers have argued against the ubiquity of these features as defining cave organisms, however, as their prevalence within the communities can be low and in some cases the troglomorphy has been shown to be relatively plastic (Romero, 2009).

Among other evolutionary responses, the lack of light within caves has implications for the behaviour of species that live therein. Troglomorphic behaviour has been observed in the form of reduction in photoresponse, aggregation behaviour, responses to alarm substances, feeding, aggression, thigmotaxis, as well as mating behaviours and disturbance reactions that differ from very similar species found in surface environments (Poulson, 1963; Plath *et al.*, 2004; Culver and Pipan, 2009; Romero, 2009). For instance, in investigating amblyopsid fish, Poulson (1963) found that the avoidance responses to disturbing stimuli of cave species were greatly reduced as well as having greater thigmotaxis. Both of these behavioural adaptations were found to be greater within troglobitic species than epigean species, with an intermediate level being found in the troglophilic species that was studied (Poulson, 1963). Another study by Plath and Schlupp (2008) found that within cave species of Atlantic mollies (*Poeceilia mexicana*) shoaling behaviour was reduced. This response was found in two distinct populations indicating that it is the cave environment itself that elicits the behavioural change (Plath and Schlupp, 2008). The authors hypothesised that it was due to increased food competition and a lack

of avian and piscine predators that selected against shoaling and relaxed selection on shoaling, respectively (Plath and Schlupp, 2008). Interestingly, there is also research to suggest that in some cave species, mating preferences may be maintained but the determination of traits sexually selected for can undergo change (Plath *et al.*, 2004). Plath *et al.* (2004) found that in *P. mexicana*, a preference for larger mating partners was maintained in the cave population. Fascinatingly, however, this preference was maintained in aphotic environments only by individuals from the cave population (Plath *et al.*, 2004). Thus, the mating preference has been maintained by the accession of non-visual stimuli to the task of determining body size (Plath *et al.*, 2004).

The physiology of species inhabiting cave environments has also been shown to be affected by the cave environment. The cave environment and the limited resources are believed by Poulson (1963) to be responsible for the lowering of metabolic rates in cave fishes. Interestingly, this reduction in metabolic rate was not related to a reduction in levels of swimming activity, and was in fact associated with an increase in swimming efficiency (Poulson, 1963). Relaxation of selection has also had an impact on species physiology underground. For example, constant high humidity may relax selection on water loss rates and cuticular permeability, the environment no longer being desiccating. Hadley *et al.* (1981) found this to be the case in an investigation of cave lycosid spiders where the cave spiders were found to lose water at a rate of approximately 5 times greater than surface spiders at a relative humidity of 50% while at 90% cave spiders gained body water (Hadley *et al.*, 1981).

Morphologically, cave species are often considered extreme. A suite of traits are considered defining in identifying "true" cavernicoles (Table 1) (Romero, 2009). Species are often classified according to their degree of troglomorphism. Commonly these categories are: troglobites, those organisms which are obligate cave-dwellers and display complete

troglomorphism in some aspect, like an absence of eyes; troglophiles, facultative or obligate organisms with some morphological features associated with cave life but not necessarily complete; trogloxenes, facultative cave inhabitants that display no troglomorphisms; and accidentals, species found underground by chance, unable to survive and reproduce underground (Culver and Pipan, 2009; Romero, 2009). Despite the prevalence of these classifications, many organisms entire life histories are contained within caves and the species may display no troglomorphism and the suite of troglomorphisms varies between "troglobites" suggesting that these labels may not be useful for classifying the cave biota (Romero, 2009). There also exists evidence that, in some cases, the troglomorphy is partly plastic. One striking result was obtained by Romero *et al.* (2002) when investigating of the effect of exposure to light during development in a cave species of fish. They found that, in the epigean sister species, there was a reduction in eye size when they were raised in an aphotic environment while in cave species raised in a photic environment, the eyes fully developed (Romero *et al.*, 2002). Some morphological features have been shown to be adaptive in other species however. As an example, Poulson (1963) found that in amblyopsid cave fish their lateral lines were more developed offering better non-visual detection of their environments. More recently, Mejía‐Ortíz *et al.* (2006) found evidence of enlarged antennae with increased setation in cave species.

In New Zealand, however, species which have developed these traits in response to a subterranean lifestyle are rare. One major group of subterranean invertebrates, the Coleptera Trechini tribe (Carabidae: Trechinae), is comprised of a large proportion of cave dwelling species, almost half the known species (May and Kermode, 1972). Many of these subterranean species display varying levels of troglomorphism with examples of depigmentation, reduced or absent eyes, and compensatory enlarged non-sensory appendages (May and Kermode, 1972). New Zealand's one cave spider does not show any troglomorphism. This species, the Nelson Cave Spider, *Spelungula cavernicola*, is the only

spider in New Zealand caves whose entire life cycle occurs inside the cave environment (Hunt and Millar, 2001). However, very little is known of this species with a single MSc making up the study done (McLachlan, 1993). Some New Zealand arthropods do display troglomorphic features, such as the sphaeromatid isopods of the *Bilistra* genus (Sket and Bruce, 2004). These arthropods display depigmentation typical of organisms considered to be cave adapted, however, this is the only known trait to have undergone a troglomorphic transformation in this group (Sket and Bruce, 2004). Although the troglobitic fauna of New Zealand is not entirely absent, these species remain exceedingly rare with a majority of cave dwelling species found in New Zealand caves troglo/stygophiles or accidentals that are facultative in the cave environment (Death, 1989; Watson, 2010).

The lack of primary production, often leads researchers to view the cave environment as resource limited. It is frequently considered to be a harsh and depauperate environment for this same reason. The dependence on surface derived detritus and production produces a gradient at the entrance of the cave of both light penetration, surface weather conditions and energy/nutrient penetration (Howarth, 1993). The gradient flows through the light zones, the entrance and the twilight zones through to the transitional and deep zones where no light penetrates (Howarth, 1993). Many studies attest to resource limitation in cave environments, with many caves resource or energy limited to some degree (Simon and Benfield, 2001; Simon *et al.*, 2003; Simon *et al.*, 2007; Culver and Pipan, 2009; Venarsky *et al.*, 2014). The low resource environment is essential for maintenance of cave communities (Wood *et al.*, 2002; Venarsky *et al.*, 2014). Where studied, the ability of cave obligate species to exploit influxes of organic material are less influential on facultative cave species (Wood *et al.*, 2002). The implications are that pollution events can displace troglobitic species, whose habitats are often fragmented and isolated, thus altering communities significantly (Barr and Holsinger, 1985; Venarsky *et al.*, 2014).

New Zealand Cave Ecology

Karstic environments are spread throughout New Zealand, in both the North and South Islands (Fig. 1). Beneath the surface of these lands lie hundreds of caves. However, despite the widespread nature of the cave environment, the New Zealand literature is surprisingly scant in its analysis of cave ecology. Most studies performed on New Zealand cave species focus on the morphology or taxonomy of cave adapted species (May and Kermode, 1972) with a few studies that focus on behaviour or ecology (Pugsley, 1984; Broadley and Stringer, 2001). Much of the ecological literature regarding cave species focusses on the impacts of tourism on the glow worm populations within the Glow worm Caves in Waitomo (e.g. Pugsley (1984) and Broadley and Stringer (2001)).

Death (1989) found that a stream flowing within a cave had similar relative abundances but at lower densities of lotic invertebrates to the inflowing surface stream. The survival of animals within the cave stream was attributed to both their ability to survive on low food levels and on their ability to drift straight through the cave (Death, 1989). Community structure in cave streams has also been studied

Figure 1: Karst regions of New Zealand, shaded (Auckland University, 2006).

in a few caves in the Waitomo region in New Zealand (Watson, 2010). Watson (2010) found that, for many species, the drift density of species on the surface was related to their benthic abundance in the caves. This was not the case for all species and neither was the relationship present in all caves. This suggests that although drift is an important

characteristic of cave stream communities , other factors can create unique cave communities (Watson, 2010). For instance, a distinct reduction in the proportion of predators and grazers within New Zealand underground communities was observed by Watson (2010). Previous authors have suggested that cave conditions like an abundance of bedrock and a reduction in prey densities make the cave environment unsuitable for many predatory species (Pekarsky, 1983; Gibert and Deharveng, 2002). Watson (2010) concluded that caves in the Waitomo region appeared to be largely structured by differential drift densities and cave tolerance of species rather than caves being structured by resource limitation.

With very little information on how the ecology of these environments responds to the changing pressures of human land use, it can be difficult to construct effective conservation management plans. The aim of this study was to investigate the trophic bases of cave stream communities in the Manawatū region of New Zealand, and investigate how agricultural land use may impact resources and/or community structure. Relationships between lotic invertebrates and environmental/habitat conditions were measured on the surface and in the caves of four streams that differed in the proportion of agriculture in the catchment. This was followed by an examination of the energetic/trophic pathways of those communities through the use of stable isotope ratios to establish if the trophic bases differ with land use.

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Table 1: Troglomorphic characters (sensu Christiansen (1962)), reproduced from Romero (2009).

Morphological	Physiological	Behavioural
Reduced or lost		
Eyes, ocelli	Metabolism	Photoresponses
Visual brain centres	Circadian rhythms	Aggregation
Pigmentation	Fecundity	Aggression
Pineal organ	Egg volume	Response to alarm
Body size		substances
Cuticles (terrestrial arthropods)		
Scales (fish)		
Swim bladder (fish)		
Enlarged		
Chemoreceptors	Life span	
Mechanoreceptors	Lipid storage	
Appendages	Metabolism	
Body size		

Chapter 2: The effect of agriculture on cave stream

invertebrate communities

Agricultural stream just upstream of cave.

Abstract

Human land use plays an important role in determining the species composition of streams draining those catchments. A number of streams in limestone areas of New Zealand also flow through caves; a fragile environment dependent on the surface for both colonists and resources. The impacts that land use changes have on cave stream faunas have not been considered widely in the literature. This study examines how agriculture may influence cave stream macroinvertebrate communities. The invertebrate communities in four cave streams and their surface counterparts were sampled in 2014/2015. These communities were examined alongside habitat quality data and GIS land use data to determine the relationship between stream communities, caves, and agricultural land use. Agricultural land use was associated with differences in both community composition and health for surface streams. These differences were less pronounced within cave communities under different land use regimes. Sedimentation was associated with changes in both community composition and health. The effect of sedimentation was the principal agricultural stressor in these cave streams. The overall effects of agriculture were lower within the cave in comparison to the surface; this is likely due to the reduced number of potentially deleterious stressors.

Introduction

Changing land use, among other things, is a major threat to all natural environments and biodiversity (Holdaway *et al.*, 2012). Historical habitat loss and deforestation has led to the local extirpation of many species, the complete extinction of others and the endangerment of entire ecosystems (Brooks *et al.*, 2002; Holdaway *et al.*, 2012). Currently, the intensification of land use to maximise productivity in New Zealand is increasing rapidly (Foote *et al.*, 2015) and there is considerable research illustrating the influences on freshwater environments (e.g. Young *et al.* (1994) & Ryan (1991)). However, one major New Zealand freshwater habitat has largely been ignored, subterranean ecosystems, such as caves and underground aquifers. The ecological processes and biodiversity of caves and other subterranean environments have not been as widely studied, perhaps because of their inaccessibility or an "out of sight, out of mind" attitude.

The effects of human land use on surface freshwater ecology and biodiversity are varied. Many of the impacts relate to the reduction in natural cover of the riparian area directly adjacent to, and upstream of the stream, as well as the addition of nutrients and sediment (Richards *et al.*, 1993). For instance, the removal of a complex and well developed riparian areas increases autotrophic organic carbon production (Bunn *et al.*, 1999). Associated with the increase in production is often a decline in stream health as primary production becomes dominated by more unpalatable plant species (Bunn *et al.*, 1999) and variations in dissolved oxygen, pH and temperature increase (Wilcock *et al.*, 1998). Deforestation of riparian zones also impacts sedimentation rates within streams (McKergow *et al.*, 2003). Anthropogenically altered sedimentation has been shown to have a wide range of negative effects on the stream biota, impacting every trophic level from primary producers to predatory fish (Ryan, 1991; Wood and Armitage, 1997). In altering the

natural surroundings of the stream, human land use often results in increases in nutrient levels within streams (Wilcock *et al.*, 2011). This increase in nutrients works in tandem with the increased insolation to exacerbate problems of increased autotrophic growth leading to eutrophication, a decrease in biodiversity and stream health (Hall *et al.*, 2001; Shilla and Shilla, 2011). For example, a study undertaken by Allan *et al.* (1997) found whole catchment land use better explains biotic integrity, habitat suitability and diversity than when only the riparian area is considered. This was due to sedimentation rates that were up to ten times greater in deforested catchments than forested catchments, along with greater nutrient levels entering streams, all together reducing habitat suitability and availability and ultimately the biotic community (Allan *et al.*, 1997).

Cave biota are usually dependent on the surface environment for inputs of energy and nutrients (Romero, 2009). In most caves, this input constitutes the main source of energy for the system (Culver and Pipan, 2009). The main point of entry of these energy sources to the cave is via stream water entering the cave, although resources also enter through percolation through the karst, and active movement of animals into the cave (Culver and Pipan, 2009). Alterations in inputs to caves can have large impacts on whole communities (Simon and Benfield, 2001; Huntsman *et al.*, 2011; Schneider *et al.*, 2011). Cave species increase in abundance and species assemblages are determined by the types of resources available within the cave (Schneider *et al.*, 2011). In fact, the dependence on surface energy results in carbon limitation in many cave systems (Simon and Benfield, 2001; Huntsman *et al.*, 2011). (Simon and Benfield, 2001) supplemented wood and leaf litter in cave streams in West Virginia and found increases in fungal and bacterial biomass indicating carbon limited secondary production. Huntsman *et al.* (2011) also found that the density, biomass and secondary production of a cave adapted salamander were greater where a larger quantity of detrital organic matter was available. These studies suggest cave

communities are structured from the bottom-up and are critically dependant on resource input from the surface.

The literature on the effects of land use on surface stream communities may provide some insight for cave stream ecosystems. For instance, one could predict that cave biodiversity would be negatively affected by sedimentation. On the surface, sedimentation results in the loss of habitat heterogeneity and smothering of food resources (Ryder, 1989; Richards and Bacon, 1994; Waters, 1995; Burdon *et al.*, 2013). Sedimentation is therefore likely to have similar negative impacts on underground communities. Furthermore, a lack of coarse particulate organic matter (CPOM) entering the stream as a result of deforestation and subsequent loss of allochthonous input is likely to impact the energy and nutrient fluxes of the cave environment. Neill *et al.* (2004) found water quality in a karst environment was contaminated by agricultural development from historical land use; contaminants included nitrate, orthophosphates, and metal in sediments. Faecal bacterial counts have also been found to increase in caves within agricultural catchments (Hunter *et al.*, 1999). Clearly agricultural activities have the potential to impact biologically important (i.e. nutrients and bacterial biomass) drivers of biological communities. (Wood *et al.*, 2008) found excessive organic pollution from a water treatment plant reduced the abundance of all species within a cave and did not recover within a year, with the dominant taxa following the event being two species of oligochaete. Surface land management affects cave invertebrate communities but how, and in what ways, is still unclear.

In this study I have addressed this question by examining differences between cave and surface stream communities under different land use regimes within the Manawatū River Catchment. I hypothesise a similar response to land use change in cave streams as in surface streams; however, the magnitude of change should be reduced because of the narrower range of potential deleterious effects.

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Methods

Study Sites

This study was conducted in four caves in the central North Island, New Zealand, each fed from upstream by a surface stream. Three of these caves are located between the Puketoi Range and the Waewaepa Range east of Pahiatua on the east coast of the North Island. The other site is north of Pohangina, near the western side of the Ruahine Ranges on the west coast of the North Island (Fig. 1). A breakdown of microhabitat distribution is given in Table 1.

Crash cave is a small cave to the south of other two Pahiatua caves. It has developed in the Te Onepu Formation limestone. Within the cave a second order stream flows, originating on the surface entirely in sheep farm.

PT17 cave is located at the northern end of the Waewaepa Range and contains a second order stream which runs into the cave from sheep farmland on the surface. This cave has been formed in the Kumeroa formation limestone and flanks the greywacke of the Waewaepa Range (Halliday, 1987). The cave has developed to contain many jointed passages which have since been abandoned by the streams.

Famous Five is located approximately two kilometres east from PT17 and has developed in the same limestone formation (Halliday, 1987). The stream that feeds into this cave is first order and drains from a small catchment of predominantly sheep farming with small patches of regenerating native forest.

Piripiri cave is located on the western side of the Ruahine range approximately 20 km north of the town of Pohangina. Within it a first order stream flows, with its origins in exotic pine and native podocarp-broadleaf forest.
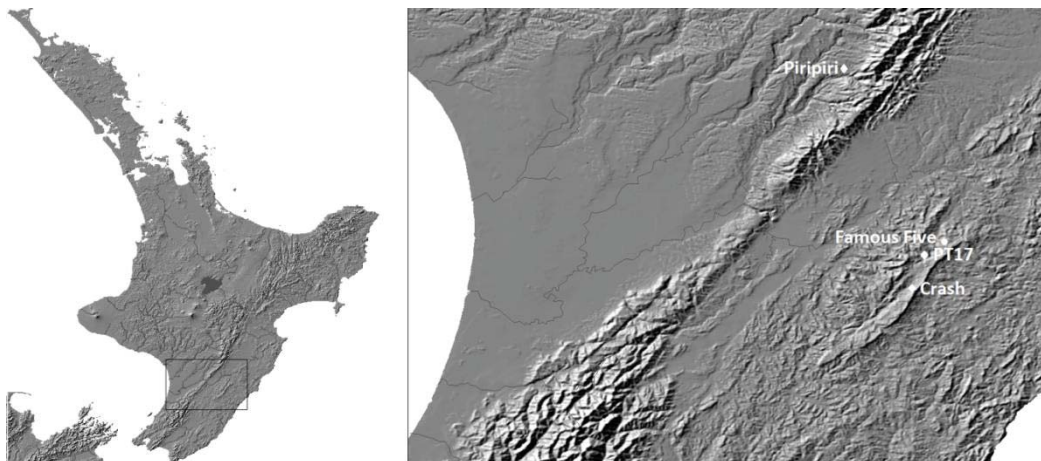
Figure 1: Location of study sites sampled between June 2014 and February 2015.

Figure 2: Cave draining an agricultural catchment. Note high stream bed sediment.

GIS data collection

Land use data was collected from the Land Environments New Zealand database (LENZ) (Leathwick, 2002) and Freshwater Environments New Zealand database (FENZ) (Leathwick *et al.*, 2010). Current land uses for both the whole catchment and riparian zones of the

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streams were determined using these databases in ArcGIS (version 10, buffer and intersect tools). A range of potential riparian zone widths were included for analysis based on commonly applied widths from the literature (10m – 45m) (Osborne and Kovacic, 1993; Parkyn and Policy, 2004).

Sampling

Cave and surface streams were sampled on three to four occasions each, between March 2014 and February 2015. Sample reaches were located 100 m from the entrance of the caves, both inside and out. Invertebrates were collected with 1-min kick nets with a mesh of 500 microns. Samples were collected from the range of available habitats in each stream.

Invertebrate samples were preserved in 70% ethanol before sorting, enumeration and identification to the lowest possible taxonomic level using Winterbourn *et al.* (1989). Guild affiliations for each taxonomic group were determined using information from the Landcare Research website (Landcare Research, 2015) and from the literature (Winterbourn *et al.*, 1984; Parkyn and Winterbourn, 1997).

Table 1: Microhabitat distribution (% pools, riffles and runs) for four Manawatū streams within the cave and on the surface.

Site	Percent Pools		Percent Riffles		Percent Runs	
	Surface	Cave	Surface	Cave	Surface	Cave
Famous Five	0	20	0	20	100	60
Crash	0	28.5	0	28.5	100	42.9
PT17	20	40	40	20	40	40
Piripiri	20	33.34	40	0	40	66.67

From each site, for both the cave and surface streams, deposited sediment was estimated visually for each stream using the Ministry for the Environment protocols (Clapcott *et al.*, 2011) as a proportion of the stream bed covered in sediment over a 25 m reach. From this same reach measurements of width, depth, conductivity and water velocity were taken to record habitat. Conductivity was measured with an Orion model 115 conductivity meter and velocity was calculated with a velocity head rod. Water from each reach was analysed for total nitrogen (TN) by colorimetric analysis and total phosphorous (TP) by automatic ascorbic acid reduction by Central Environmental Laboratories. Particle size distribution was measured with a gravelometer to characterise 100 particles into phi class collected over a 25 m reach.

Data analysis

Environmental differences between the cave and surface streams were examined with paired t-tests for each measured variables.

Differences in biological metrics (QMCI (Stark, 1985), %EPT family richness, Simpson diversity (Simpson, 1949), Pielou's evenness (Pielou, 1975), Shannon diversity (Shannon and Weaver, 1949)) between cave and surface streams and catchment types were analysed with ANOVA using the "Stats" package in R (R Core Team, 2013).

Model selection for determining the variables most important in determining stream health, measured as QMCI, was achieved using stepwise regression in R using the step function in package "Stats" (R Core Team, 2013). The global model was built using all variables that were not auto-correlated. For auto-correlated variables only one was included. Further investigation of the relationships that were found important by stepwise regression was assessed with simple regression models.

Differences between communities found under different conditions (i.e. cave/surface, agriculture/forest) were initially assessed using an ANOSIM in package "Stats" in R (R Core Team, 2013). This was done for both species composition and for guild proportions. Community differences were quantified by calculating Bray-Curtis dissimilarity scores (Bray and Curtis, 1957) for the communities using the R package "Vegan" (Oksanen *et al.* (2008). Non-metric multidimensional scaling (NMDS) was used to visualise and investigate how community composition differs across caves and land use. Potential environmental drivers of community composition were examined using the function "Envfit" in the package "Vegan" (Oksanen *et al.*, 2008). NMDS and environmental vector fitting was also performed for guild compositions of communities using the same methods.

The contribution of different species or guilds to differences between communities was determined using similarity percentage (SIMPER) analysis in R, package "Vegan" (Oksanen *et al.*, 2008). A SIMPER analysis finds the contribution of these species to the difference between communities. The SIMPER analysis was performed to evaluate the contributions

of species and guilds to both differences between the surface and cave communities as well as between systems dominated by agriculture and native forest.

Results

There were no significant differences in any habitat variable between streams (all t test p-values >0.1, Table 2, Fig. 3).

Increasing sediment levels related to a decrease in QMCI (r^2=0.41, df=26, p=<0.001, Fig. 4) and a decrease in EPT (r^2=0.36, df=25, p=0.002). QMCI differed between sites but was always highest in the PT17 and Piripiri cave streams (Fig. 3, $F_{2,25}$=5.3, p=0.006). QMCI did not differ between cave and surface environments (F_1=1.25, p=0.27). The most parsimonious model for predicting QMCI was proportion of sediment in the stream along with TN, riparian land-use and water velocity (R^2=0.37, $F_{2,26}$=9.339, p=0.005). The response of EPT to an increase in sediment was humped, but declined at higher levels of sediment (Fig. 4, r^2=0.34, p=0.002). Stepwise regression found that the same variables that best predicted QMCI were also useful for EPT along with TN, riparian land-use and TP (R^2=0.5, $F_{5,23}$=6.159, p<0.001). EPT values were not different within the caves in comparison to the surface (F_1=1.82, p=0.07).

Species compositions of communities were not significantly different between cave and surface sites (ANOSIM R = 0.0, p= 0.57). However, Guild composition differed between surface and cave environments (R=0.1, p=0.04). Between agriculture and forest dominated catchments species compositions were significantly different (ANOSIM R=0.40, p=0.001) as well as guild compositions (ANOSIM R=0.36, p=0.001). Communities were strongly linked to land use of the surrounding catchment with different land uses having distinct communities (Fig. 5, Table 3). SIMPER analysis identified a decrease within the caves in *Deleatidium* (contribution = 0.27, p=0.02) and in *Potamopyrgus* (contribution = 0.25, p= 0.003) which

accounted for 55.31% of the variation between cave/no cave communities with rarer species accounting for less than 9% each.

Table 2: GIS and in stream variables for each reach. Prop. Sed. = Proportion deposited sediment on stream bed, Rip. = Riparian. Units for total nitrogen and total phosphorus are g/m3.

Site	Cave				Surface			
	Crash	Famous Five	Piripiri	PT17	Crash	Famous Five	Piripiri	PT17
Prop. Sed.	0.5	0.3	0.01	0.05	0.9	0.8	0.2	0.3
Total Nitrogen	0.2	0.76	1.7	0.99	0.27	0.83	0.3	0.24
Total Phosphorous	0.02	0.02	0.06	0.03	0.01	0.02	0.01	0.02
Exotic Grassland	1	1	0.5	0.24	1	1	0.5	0.24
Exotic Forest	0	0.003	0.21	0.04	0	0.003	0.21	0.04
Native Forest	0	0	0.29	0.7	0	0	0.29	0.7
Natural Cover	0.05	0	0.28	0.7	0.05	0	0.28	0.7
Rip. Indigenous Forest	0	0	50	74	0	0	50	74
Rip. Exotic Grass	100	100	21	18	100	100	21	18
Rip. Exotic Forest	0	0	23	7	0	0	23	7
Annual Rainfall (mm)	1857	1747	2131	1747	1857	1747	2131	1747
Velocity(cm/sec)	5.64	4.85	6.57	4.00	4.08	5.6	6.18	6.57
Width(cm)	58.8	65	70	106.4	72.2	85.6	36.2	105.4
Cond (μS)	285.8	361	170.82	206.2	284.6	363.8	85.62	116.26
Depth (cm)	22.2	18.2	35.55	15.1	20.9	27.2	30.29	11.7
Particle Size (D50)	48	48	24	24	1	32	48	24

Results for the guild structure analyses show a similar link to the catchment as the species (Fig. 6, Table 4). High intensity and low intensity land uses grouped together. Pasture and increased sedimentation was associated with one group while forested catchments

(indigenous and exotic) were associated with another (Fig. 6). Riparian zone land use was less powerful in explaining community patterns, the only significant predictor of guild structure being riparian exotic forest ($R^2 = 0.25$, p = 0.028, Table 4). In addition, the vector fitting analysis supported the ANOSIM in showing that guild proportions within a cave are significantly different to those found on the surface ($R^2 = 0.1$, p = 0.05). The guild differences with the most contribution to the differences among guild communities are scrapers, contributing 30.45% with their decrease in number within the caves.
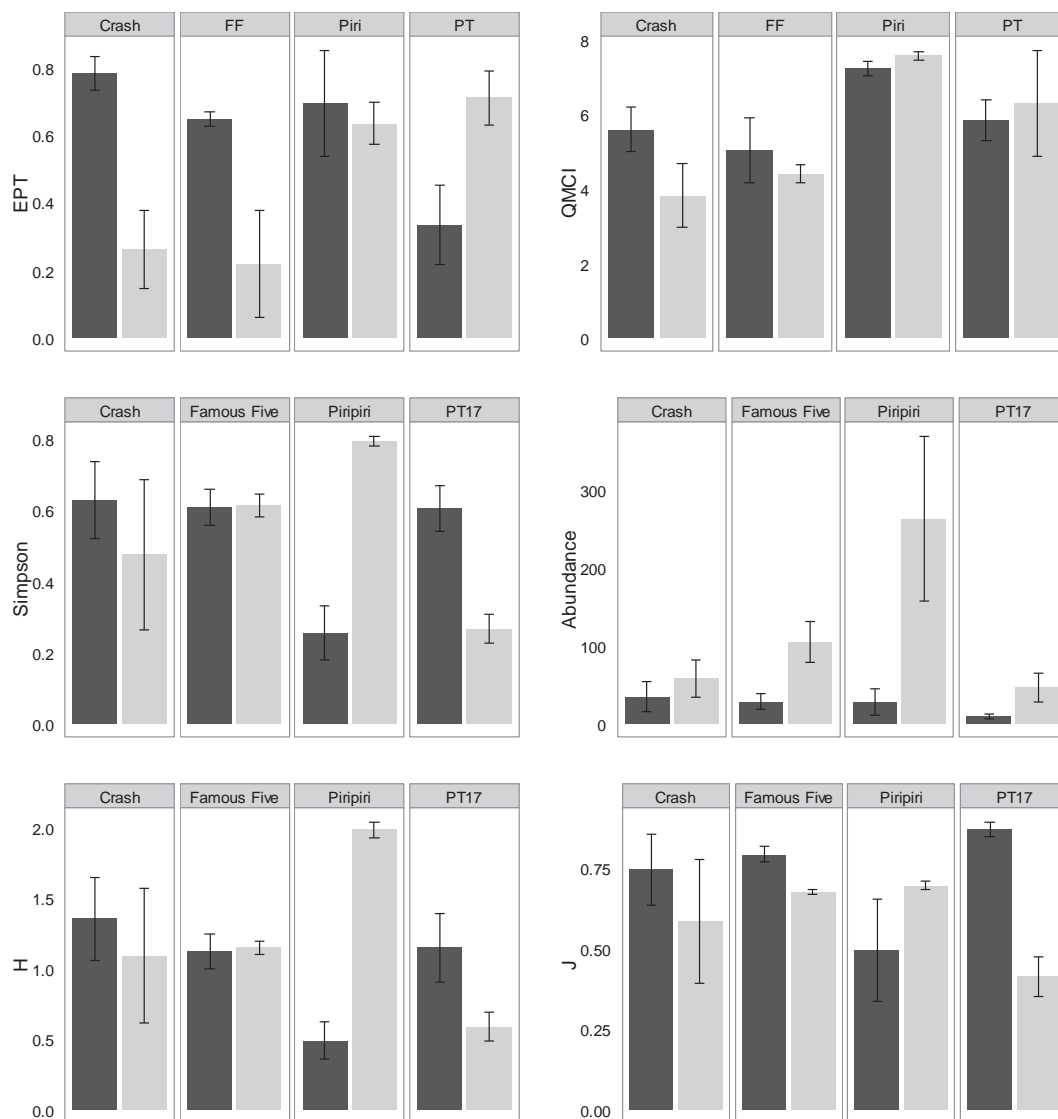
Figure 3: Diversity and health metrics for invertebrate communities collected in cave and surface reaches between 2014 and 2015.QMCI scores for Cave (grey bars) and Surface (white bars) sites.

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Two way ANOVA (QMCI vs. Cave/Surface and Dominant catchment cover interaction term):

$F_{2,25}=5.3$, $p=0.006$., Two way ANOVA for EPT: $F_{2, 25}= 7.3$, $p=0.001$. Abundance was significantly higher for non-forested sites.
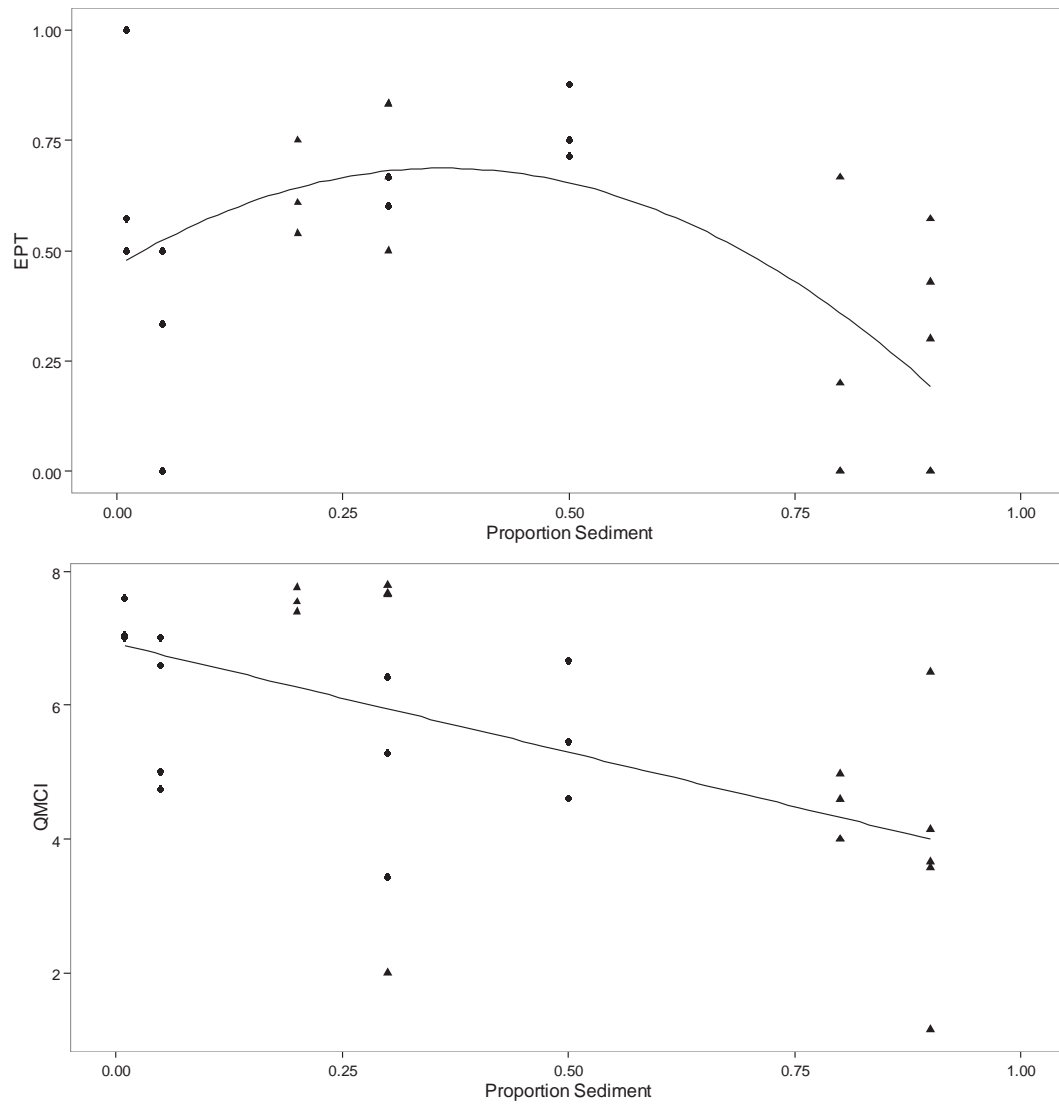
Figure 4: QMCI and EPT plotted against proportion of the stream bed covered in sediment for cave and surface stream communities. Diamonds are cave sites and triangles are surface. EPT: $R^2= 0.34$, $p= 0.007$; QMCI: $R^2= 0.32$, $p<0.001$.

Table 3: Correlation of habitat variables and NMDS axes for an ordination of stream invertebrate communities collected at 4 cave and surface streams in forest and pasture in 2014. Vectors plotted on figure 5. Significance at 0.05 = *, 0.01 = **, 0.001 = ***

Independent Variable	r^2	significance	P
Cave	0.10		0.25
Proportion Sediment	0.47	***	0.0007
High Prod Grassland	0.49	***	0.0004
Exotic Forest	0.24	*	0.03
Low Prod Grassland	0.34	**	0.0024
Natural Cover	0.45	***	0.0004
Total Phosphorous (TP)	0.29	**	0.015
Total Nitrogen (TN)	0.17		0.09
Average Annual Rainfall	0.10		0.25
%Riparian Grassland (RipHPEG45)	0.48	***	0.0004
%Riparian Indigenous Forest	0.49	***	0.0004
%Riparian Exotic Forest	0.28	*	0.015
Velocity	0.27	**	0.01
Stream Width	0.1		0.27
Stream Depth	0.15		0.12
Conductivity	0.36	***	0.001
Sediment Particle Size	0.22		0.052
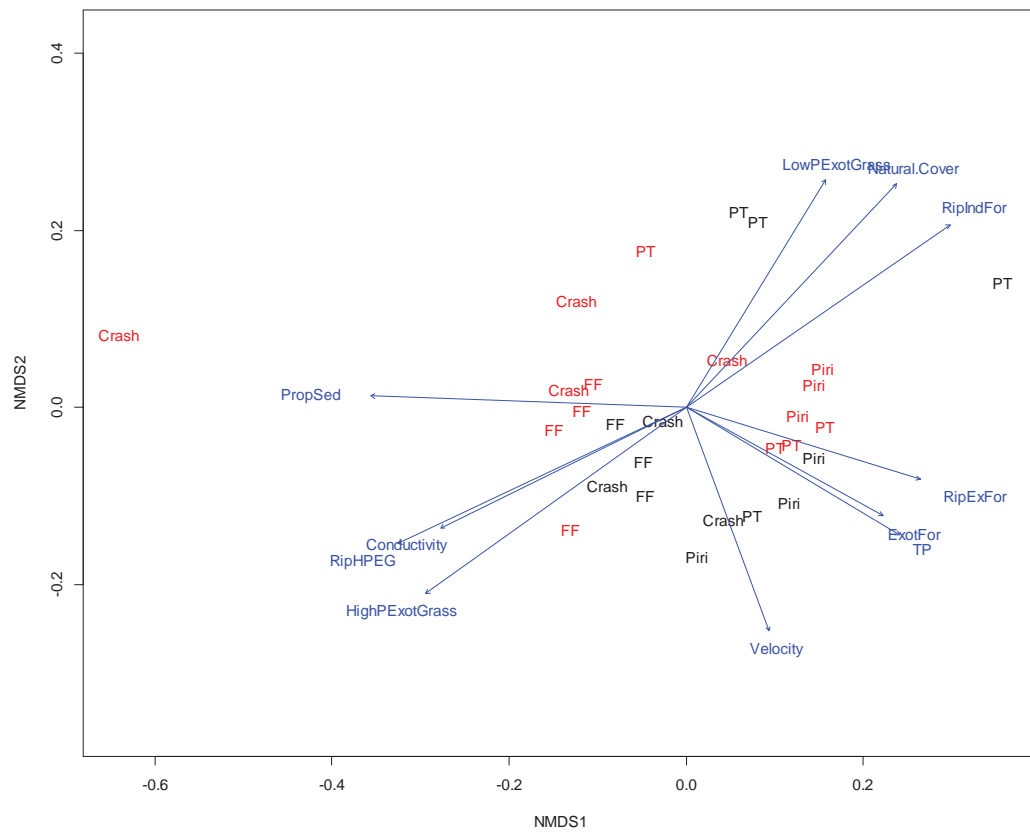
Figure 5: NMDS of cave (red) and surface (blue) invertebrate stream communities from 4 Manawatū streams. Stress=0.12. Vectors are significant predictors at p<0.05, with the associated R2 and p-values presented in Table 3.

Table 4: Correlation of habitat variables and NMDS axes for an ordination of guild proportions for communities collected at 4 cave and surface streams in forest and pasture in 2014. Vectors plotted on figure 6. Significance at 0.05 = *, 0.01 = **, 0.001 = ***.

| Independent Variable	r^2	Significance	P
Cave	0.25	*	0.03
Proportion Sediment	0.50	***	0.0004
High Prod Grassland	0.63	***	0.0004
Exotic Forest	0.18		0.07
Low Prod Grassland	0.46	**	0.0012
Natural Forest	0.61	***	0.0004
TN	0.10		0.26
TP	0.18		0.08
Average Annual Rainfall	0.24	*	0.028
%Riparian Native Forest	0.19		0.065
%Riparian High Prod Grass	0.13		0.15
%Riparian Exotic Forest	0.25	*	0.027
Velocity	0.25	*	0.04
Stream Width	0.3	*	0.01
Stream Depth	0.05		0.47
Conductivity	0.45	***	0.0008
Sediment Particle Size	0.18		0.075
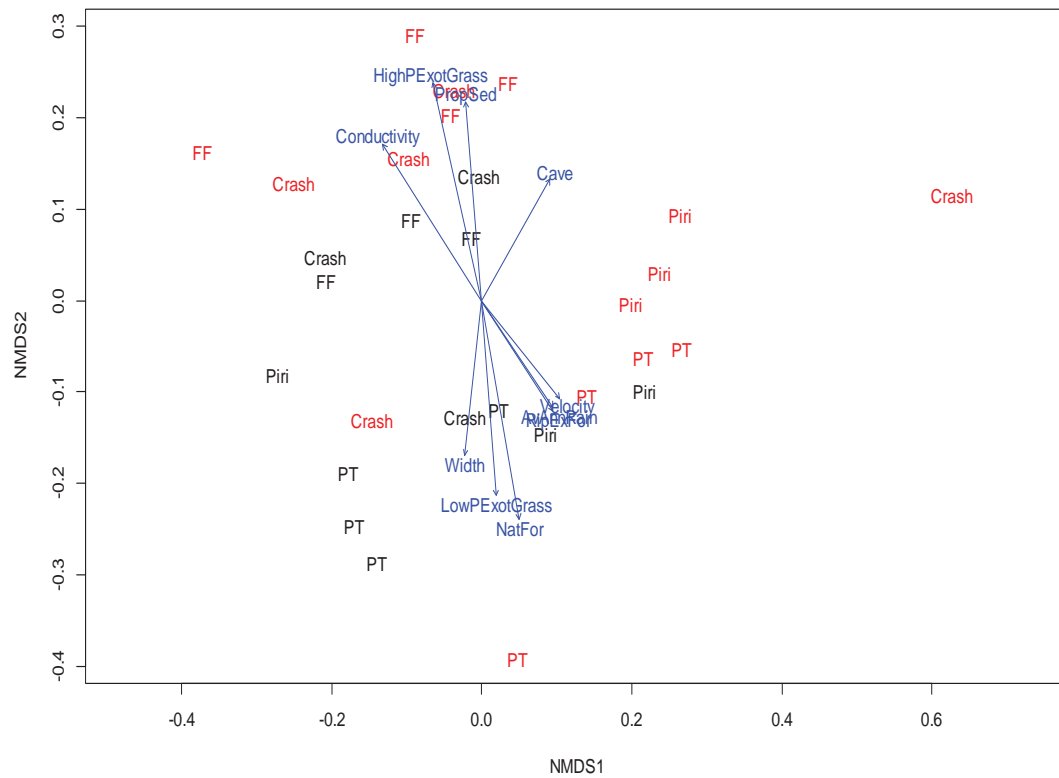
Figure 6: NMDS of guild relative frequencies of invertebrate stream communities from 4 Manawatū

streams. Stress=0.16. Blue vectors are significant predictors at p<0.05, R^2 and p values presented in

Table 4.

Discussion

The stream invertebrate species in the cave communities were no different from the surface communities. Clearly the cave ecosystems are an extension of surface stream communities (Culver and Pipan, 2009; Watson, 2010). Not surprisingly the impacts of land use on the cave communities are similar to those affecting the surface stream communities. However, the impact of agriculture was less dramatic within the caves possibly because of the redcued effect of elevated primary production affecting the surface (e.g. eutrophication, dissolved oxygen levels from photosynthesis) (Quinn *et al.*, 1997; McDowell *et al.*, 2009). Although the impacts were lesser on the cave stream community, surface land management decisions still impact the cave communities. The caves altered the guild composition of the communities and this probably moderated the influences of agricultural land use on the communities therein. The reduction in QMCI with land use / sediment deposition is much more pronounced on the surface. The results of this study suggest that communities of cave streams are not impacted by the full range of stressors of human activity which have been experienced by their surface counterparts.

The community composition within the caves was very similar to that in the corresponding surface stream. The main differences between the two environments seemed to be in functional feeding groups that differed in relative abundance. As the difference in guild composition was small (ANOSIM R=0.1) the difference found despite the lack of difference in species composition between the communities may be the result of an accumulating number of undetectable differences between species in different feeding groups. The main contributor to the difference in community guild structure was an increase in proportion of scrapers (e.g. *Deleatidium*). This reflects differences in food availability and is examined in more detail in chapter three. Several studies have found epilithic biofilm is a more

important food source in caves than outside (Watson, 2010). In addition, even where other resources are abundant within caves, biofilm may be preferred as an energy resource by many invertebrates. Simon *et al.* (2003) illustrated this with carbon tracer experiments tracking carbon sequestered by biofilms and finding they were incorporated throughout the community. It has been suggested that the resource limitation found within caves and the lack of primary results in reduced numbers of predators or their complete absence (Gibert and Deharveng, 2002), although that was not the case in these cave streams. However, other New Zealand studies have found this and Watson (2010) found that predators were rare within Waitomo cave streams.

It is important to consider the catchment and riparian areas when studying lotic ecology. This wider scale perspective has resulted in theoretical and practical advancement in the study and restoration of many stream environments (Allan *et al.*, 1997; Gergel *et al.*, 2002; Roy *et al.*, 2003; Allan, 2004). A wider scale catchment view has not been considered in cave stream communities before; thus the role of extra lotic environments in the determination of cave stream communities. The results presented here provide evidence that the composition of the riparian habitat has an important role in determining the composition of species in underground communities and that guild composition is related to whole catchment uses of land. The data also suggest that riparian level variables are important for determining cave stream health, measured as %EPT. Previous research has shown that surface pollution events can influence communities in subterranean habitats. For instance, Simon and Buikema Jr (1997) found that surface septic system effluent pollution in a cave system was damaging to crustacean communities with amphipods being entirely displaced from some pools by pollution. These pollution events resulted in increased nutrient levels, faecal coliforms, and reduced dissolved oxygen (Simon and Buikema Jr, 1997). Wood *et al.* (2008) found varied responses to organic pollution within Peak-Speedwell Cavern system in the UK. Both pollution events resulted in increased

dominance, reduced species richness and reduced Shannon-diversity, the point of difference in the responses being the immediate response of the community following the events (Wood *et al.*, 2008). In one instance, elimination of almost all taxa occurred while in the other pollution tolerant taxa increased in abundance greatly (Wood *et al.*, 2008). Pollution events clearly have markedly different outcomes on cave communities, but are often deleterious.

In the present study, sedimentation was found to influence both surface and cave stream environments. However, cave streams had consistently lower values of sediment and so less impact was seen. This may be due to limited transport of sediment into the cave (White and White, 1968). Studies on sediment transport in karstic environments found that sediment transport is only achieved at any appreciable rate within complex cave channels under high flow conditions (White and White, 1968; Bosch and White, 2004). Sedimentation is well known to cause a variety of effects in stream communities where it has been studied in surface streams (Quinn and Hickey, 1990; Ryan, 1991; Quinn *et al.*, 1992). Sediment deposition increases drift propensity in many species (Suren and Jowett, 2001) and can also result in infilling of interstitial spaces, reducing habitat availability (Ryder, 1989; Ryan, 1991; Richards and Bacon, 1994). It may also change the chemical composition of water by depleting oxygen (Ryan, 1991). The degree and extent to which sediment was found to be related to community composition and health in this study suggests that interstitial habitat loss and sedimentation may be the most important impact of human land use on cave streams in New Zealand.

An interesting result of this study was the differential response of the cave health (%EPT and QMCI) to land use regimes in comparison to that found for surface communities. The result found on the surface was that sites under the most altered land use had significantly lower QMCI scores and percent EPT. This is a result that has been found repeatedly for

streams on the surface (Quinn and Hickey, 1990; Quinn *et al.*, 1992; Quinn *et al.*, 1997; Scarsbrook and Halliday, 1999; Hall *et al.*, 2001; Townsend *et al.*, 2004). These reductions are related to riparian quality (Scarsbrook and Halliday, 1999), sedimentation, insolation, and habitat quality (Quinn *et al.*, 1992). In contrast, however, the relationship between cave QMCI and land use regime was not so clear cut. The trend was towards a negative impact, reduced in comparison with the surface, but non-significant. EPT and QMCI scores in the developed sites were as high as those in forested sites. This result was surprising given the impacts that are often found in surface streams (Bunn *et al.*, 1999; McKergow *et al.*, 2003; Wilcock *et al.*, 2011), the dependant nature of cave streams on their surface counterparts (Culver and Pipan, 2009), and also due to the effects that factors associated with land use have been shown to have on cave streams, for instance Simon and Benfield (2001). The result is likely due to a reduced amount of sediment within the caves and the fact that nutrient related impacts, such as eutrophication, are unlikely to be important without photosynthesis. Sedimentation is a result of agricultural land use that is known to cause adversity for stream communities (Quinn *et al.*, 1992). Given that the effects of this (food smothering and habitat loss, among others) are unrelated to photosynthetic activity, one might expect that the impacts would be similar to what would be found for the surface. A definite impact, but with reduced intensity of sediment is what was found here, likely due to a limited ability for sediment transport through complex channels (White and White, 1968). A major impact of agriculture on surface stream macroinvertebrate communities comes the loss of the riparian zone and associated increase in macrophyte and algae growth (Quinn and Hickey, 1990; McDowell *et al.*, 2009). Noting this, a lower effect of surface deforestation on cave communities is likely considering the lack of photosynthesis. However, the loss of CPOM from a full riparian zone as resources for a wide range of species is an outcome of riparian deforestation that would likely impact the cave communities. CPOM is utilised in hypogean communities (Simon and Benfield, 2001),

and so with the removal of inputs from upstream, the source for these resources within the caves is removed. That cave communities appeared to fare better under agricultural land practices than their surface counterparts is likely a result of a limited capacity for sediment transport and a lack of impact from primary production related changes within the cave.

To summarise, agricultural land use within karst catchments has a reduced impact on the invertebrate communities in cave streams compared to those in surface streams. This study found that, within a dominantly agricultural catchment, where a surface stream might be extremely degraded, a subterranean stream is more resistant and has health measures more similar to those found in forested and/or less impacted catchments. However, the changes that do occur are similar qualitatively to what would be found on the surface, indicating that cave streams are not completely immune to the negative impacts of agriculture on freshwater ecosystems. The smaller response of cave streams to the effects of agricultural land use is likely due to the divorced spatial relationship between the environments and the lesser number of potential drivers of change. The provision of ecosystem services through a range of processes as well as a desire to preserve biodiversity means that it is important to know how these changes may be impacting on the communities that inhabit these subterranean environments.

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Chapter 3: The effect of agriculture on cave stream energy sources

The depths of Piripiri cave

Abstract

The stream environment is intimately linked with its wider catchment for the maintenance of an environment that supports a healthy biota. Importantly, for many streams, the extra lotic environment provides an input of resources that drive production within the stream. In converting catchments to increase food production these links are often broken, eliciting a change in the trophic base of the stream community. This is well documented for surface streams However, for cave streams and their communities, especially in New Zealand, very little is known of the impacts of agricultural production on cave stream trophic pathways . This is the focus of the present study where I examine how energy pathways between communities in streams draining a forested catchment differ from those draining agricultural catchments. This is addressed by examining stable isotope ratios of carbon and nitrogen of species and their resources in cave and surface streams that differ in the amount of catchment in forest versus agriculture. Agricultural communities were found to be more reliant than forested communities on autochthonous energy from epilithic biofilm, both for caves and surface streams. Conversely, coarse particulate matter was more important for those communities in streams draining forested catchments than for those in agriculture. This reflects the situation in surface streams where increased agriculture in a catchment means a greater reliance on autochthonous energy. Thus, land management practices on the surface are highly likely to impact on the communities in the caves beneath.

Introduction

Biodiversity in cave streams has received limited attention from the scientific community (Chapter 1). Cave streams provide a unique environment for unusual species the world over (Culver and Pipan, 2009). The unique selection pressures found within the subterranean environment have developed peculiarities for the biota that are rare in other environments (Romero, 2009). Much of the focus has been on adaptations of species to life in the harsh environment of the cave (e.g. Mejía-Ortíz *et al.* (2006), Poulson (1963)). Adaptations such as the loss of eyes, increased length of limbs and mechanoreceptors, and increased chemoreceptor sensitivity have enthralled researchers (Romero, 2009). In addition, the depauperate environment with its reduced numbers of species can provide useful model systems for examining ecosystem processes in a natural environment. However, little is known of the New Zealand cave biota and ecology.

Waterways free from the influence of human activity often have higher ecological health, greater diversity, and species richness (Allan, 2004). These waterways interact with surroundings that are more diverse than agricultural land further increasing the biodiversity for both stream and surface environments (Ward *et al.*, 1999; Sabo and Power, 2002; Ballinger and Lake, 2006). The health and diversity of a stream ecosystem is intimately linked to the health and diversity of the surrounding catchment (Allan, 2004). The surrounding riparian vegetation controls resource inputs, sedimentation and shading (Allan, 2004). Cave environments are even more dependent on inputs from the surrounding catchment via their inflow streams. Caves are intimately linked to the surrounding catchment and the resources they supply (Culver and Pipan, 2009; Romero, 2009). In fact, the majority of energy in cave stream communities originates at the surface and moves into the cave (Simon *et al.*, 2003; Culver and Pipan, 2009; Romero, 2009).

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Therefore it is reasonable to expect that any alteration to the surface environment will impact cave communities.

Agriculture above ground impacts water chemistry and physical habitat in streams. For example, the availability of interstitial spaces is reduced through increased sedimentation (Ryan, 1991; Neill *et al.*, 2004). Among the differences observed between forested and agricultural streams is a shift of the resource bases of stream communities from allochthonous to autochthonous dominant, with an associated change in the invertebrate community (Winterbourn *et al.*, 1984; Benstead and Pringle, 2004). This involves a change in the abundance of feeding types and the ability of particular species to thrive (Winterbourn *et al.*, 1984; Benstead and Pringle, 2004). Land use changes often coincide with a reduction in species diversity in the riparian zones of impacted streams; total macroinvertebrate abundance, diversity, and richness (Lecerf *et al.*, 2005). Pollution events on the surface are known to impact cave communities by altering water chemistry and the physical characteristics of streams (Simon and Buikema Jr, 1997; Graening and Brown, 2003). Most research investigating impacts of pollution on cave systems have found moderate nutrient pollution may increase richness and abundance of species in caves while heavy organic pollution (paper pulp and organic rich peat) was found to have negative impacts (Holsinger, 1966; Simon and Buikema Jr, 1997; Wood *et al.*, 2008).

Stable isotope analysis is a technique for analysing long term dietary composition of species that can be used to investigate food web and energetic pathways in communities (Winterbourn *et al.*, 1984; Simon *et al.*, 2003; Layman *et al.*, 2012). Studies of energetic pathways in caves using stable isotopes have found similar numbers of trophic levels below ground as above. The importance of epilithic biofilms, fed by Dissolved Organic Matter, is high in cave communities. Coarse particulate organic matter (CPOM) from the surface is not always important for cave communities (Simon *et al.*, 2003). Stable isotope analysis has

also been used to detect differences in community structure and energy pathways in the presence of land use stressors (Bunn *et al.*, 1997; Benstead and Pringle, 2004). Using stable isotope data, one can determine the importance, assimilation, and use of basal resources in a community and thus help to determine differences between communities that are driven by resource differences (Bunn *et al.*, 1997; Layman *et al.*, 2012).

Caves represent a heterotrophic extreme on a continuum of stream metabolism models from streams fed entirely through autotrophic production to those dependent on allochthonous production. The aim of this study was to investigate the relative importance of basal resources from the surrounding catchment and in cave sources for four cave stream communities. It is hypothesised that the surface community is driven predominantly by autotrophic production. In contrast, in cave heterotrophic production will dominate the energy source for the cave community. I also hypothesise an important role for allochthonous dissolved organic carbon (DOC) available to the macroinvertebrate community as epilithic biofilm and fine particulate organic matter (FPOM) in the cave.

As cave streams are dependent on the surface for inputs of many resources to sustain communities in this environment, changes in the surface environment are likely to be reflected in the underground biota. However, as communities within caves are reliant on surface streams for inflow of individuals and species as well as resources, a smaller, subset version of a heterotrophic stream might be expected from a cave being fed from a largely autochthonous system upstream. In addition to these similarities, differential penetration distances of particles and resources of different sizes are hypothesised to reduce the role of certain resources (viz. CPOM, FPOM), compared to the surface.
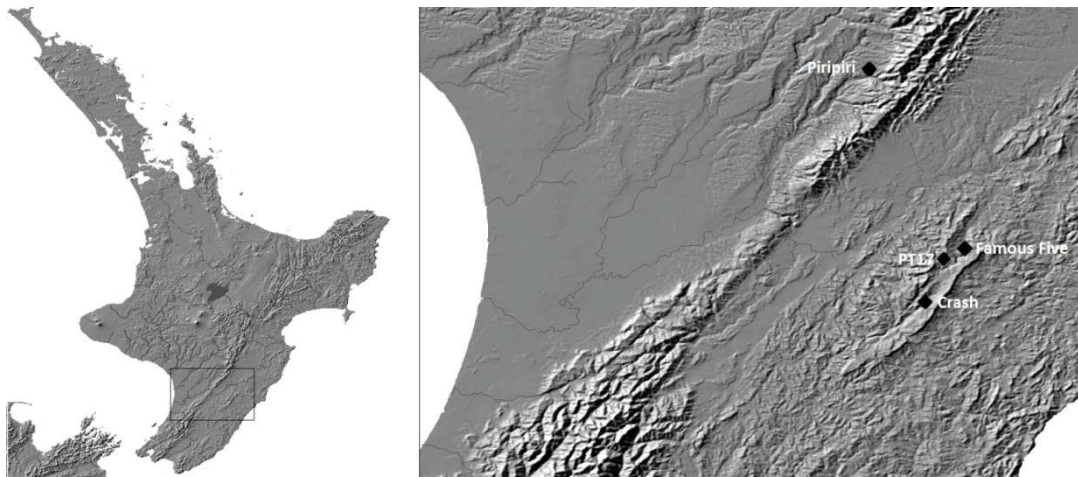
Figure 1: Location of study sites sampled between June 2014 and February 2015.

Methods

Study Sites

This study was conducted in four caves in the central North Island, New Zealand each fed by a surface stream. Three of these caves are located between the Puketoi Range and the Waewaepa Range east of Pahiatua on the east coast of the North Island. The other site is north of Pohangina, near the western side of the Ruahine Ranges on the west coast of the North Island (Fig. 1, Table 1).

Crash cave is a small cave that has developed to the south of Famous Five and PT17. It has developed in the Te Onepu formation limestone. Within the cave a second order stream flows, originating in sheep farmland.

PT17 cave is located at the northern end of the Waewaepa Range and contains a second order stream which runs through sheep farmland on the surface. This cave has been formed in the Kumeroa formation limestone and flanks the greywacke of the Waewaepa Range (Halliday, 1987). The cave has developed to contain many jointed passages which have since been abandoned by the streams.

Famous five is located approximately two km east from PT17 and has developed in the same limestone formation (Halliday, 1987). The stream that feeds into this cave is first order and drains from a small catchment of predominantly sheep farming with small patches of regenerating native forest.

Piripiri cave is located on the western side of the Ruahine range approximately 20 km north of the town of Pohangina. Within it a first order stream flows with its origins in exotic pine and native beech forest.

Table 1: Latitude and Longitude of cave stream sites.

Site	GPS Coordinates (S, E)
Crash	-40.485173, 176.075550
Famous Five	-40.429245, 176.113563
PT17	-40.431661, 176.094358
Piripiri	-40.038193, 175.977156

Sample Collection

The streams were sampled inside and upstream outside of the cave on three occasions between March and July 2014 and again during February 2015. Each reach sampled was 50 m inside or outside of the cave entrance. Invertebrates were collected with a 1-min kick net (mesh of 500 μm). Samples were taken from the range of available habitats at each site (i.e. riffles, runs and pools, Table 2). Invertebrate samples were preserved in 70% ethanol before sorting, enumeration and identification using Winterbourn *et al.* (1989) to the lowest possible taxonomic level. The number of individuals (1 – 40) used for stable isotope analysis varied with taxa, as some had low abundance. Guild affiliations for each taxonomic group were determined using information from the Landcare Research website (Landcare

Research, 2015) and from the literature (Winterbourn *et al.*, 1984; Parkyn and Winterbourn, 1997).

The dominant land use was established for each site using GIS site data from the Land Environments New Zealand database (LENZ) (Leathwick, 2002) and Freshwater Environments New Zealand database (FENZ) (Leathwick *et al.*, 2010). Stream centrelines were collected from Land Information New Zealand (Land Information New Zealand, 2014) and catchment polygons were from Ministry for the Environments REC database (Ministry for the Environment, 2014).

Table 2: Percentage of microhabitat (e.g., runs, riffles and pools) at each sampling site.

Site	Percent Pools		Percent Riffles		Percent Runs	
	Surface	Cave	Surface	Cave	Surface	Cave
Famous Five	0	20	0	20	100	60
Crash	0	28.5	0	28.5	100	42.9
PT17	20	40	40	20	40	40
Piripiri	20	33.34	40	0	40	66.67

Samples of CPOM, FPOM, and stone surface biofilm were also collected from each site, inside and outside the cave. FPOM samples were collected using a 10 cm diameter pipe pressed into the sediment. CPOM samples were collected by hand. These were transported to the lab where they were frozen until analysis. Biofilm was collected from 10 submerged rocks from inside and outside each cave. The rocks were collected in the field and biofilm was removed in the lab by brushing the rocks in a small amount of distilled water. This water was then filtered through pre-ashed glass filter paper (GFC; size = 47mm) and dried for 65 hours at 70°C before weighing. FPOM samples were washed with 30% HCl to remove

inorganic carbon present in cave sediments in the form of $CaCO_3$ which can affect isotope ratios (Simon *et al.*, 2003). FPOM and CPOM were subject to the same drying regime before being weighed. CPOM was ground with a mortar and pestle, assisted by liquid N, and weighed. Invertebrate samples were freeze dried overnight before weighing. All stable isotope analysis was achieved by combustion on a Eurovector elemental analyser coupled to an Isoprime mass spectrometer. Results are reported with respect to VPDB and N-air, normalised to Leucine (-23.0‰ δ^{13}C, 2.0‰ δ^{15}N) as an internal standard. Stable isotope ratios are expressed as δ^{13}C or δ^{15}N according to:

$$Isotope = \left(\frac{R_{sample}}{R_{standard}} - 1\right) * 1000$$

where R_{sample} is the ratio of carbon 13 to carbon 12 or the ratio of nitrogen 15 to nitrogen 14 and $R_{standard}$ are these ratios for the standard, leucine.

Stable Isotopes

For each site, community metrics were calculated following Layman *et al.* (2007). Isotopic ratio ranges were calculated for both δ^{15}N (indicator of relative number of trophic levels) and δ^{13}C (indicator of relative number of basal resources)(Layman *et al.*, 2007). Total convex hull areas were calculated in isotope space (niche space index) along with mean distances to centroids (average trophic diversity) and mean nearest neighbour distances (species packing) (Layman *et al.*, 2007). To test differences between these metrics between cave and surface environments a paired t test on the mean contributions was conducted in R (R Core Team, 2013).

Trophic levels for species were calculated using the δ^{15}N values against a species specific baseline gleaned from feeding mode (Landcare Research, 2015) with the equation:

$$Trophic\ position = [(species\ \delta^{15}\ N - base\ resource\ (\delta^{15}\ N)\ /3.5] + 1$$

after Vander Zanden *et al.* (1997). Enrichment values for δ^{15}N was 3.5‰ as per Vander Zanden *et al.* (1997). Any differences in the distribution of trophic levels between cave and surface environments or between agricultural and forested catchments were assessed with a Kolmogorov-Smirnov test in R (package stats, R Core Team (2013)).

The importance of each basal resource was inferred using stable isotope ratios of carbon and nitrogen (δ^{13}N/δ^{12}C). Analysis of these ratios was performed using package "siar" in R (Parnell *et al.*, 2008). The contribution of each basal resource to the isotopic signature of each species was calculated in R using the package SIAR (Parnell *et al.*, 2008) with a Markov Chain Monte Carlo (MCMC) on a Dirichlet prior distribution. In turn, the combination of lower trophic levels to higher trophic level invertebrates was determined with the same method (MCMC in siar, Parnell *et al.* (2008)). Trophic enrichment was assumed as in Vander Zanden *et al.* (1997) and France and Peters (1997) for fresh water ecosystems of 3.5‰ for δ^{15}N and 0.2 ‰ for δ^{13}C. Higher trophic level species were incorporated into the mixing models with an enrichment factor for δ^{15}N and δ^{13}C of:

$$E_j = E_i * \text{Trophic level}$$

Where E_i is the trophic enrichment factor as per the literature, E_j is the enrichment factor of the higher trophic level species and the trophic level is calculated as per Vander Zanden *et al.* (1997)

Differences between contributions of each of the basal resources between cave and surface communities was determined using a t test in r (package stats, R Core Team (2013)). Differences in the mean contributions, weighted by abundance, to communities for each of the measured resources were determined using an ANOVA followed by a post hoc pairwise t test in R (R Core Team, 2013). To investigate the relationship between dominant catchment cover and cave presence on the utilisation of different resources by

communities, a two way within sample ANOVA was performed on the average contributions with a post hoc Tukey's HSD test where the interaction term was significant. Utilisation of resources by species was examined using Wilcoxon rank sum tests in R to determine differences in resource use across catchment types and above and below grounds (R Core Team, 2013).

Results

Community metrics did not differ between inside and outside the caves or catchment types (Table 3). Cave communities had a significantly higher average δ^{15}N value overall (t = 4.08, df = 55.97, p = 0.00015). Caves had on average 4 trophic levels, as estimated by δ^{15}N values, while surface communities had 2.75. The distribution of species among these trophic levels was not detectable different between cave/surface nor agricultural/forested (Fig. 2). However, these differences were not significant (t=-0.06, df=3, p=0.9). There was no difference between agricultural catchments, with an average 3.5 trophic levels, and forested catchments with 3 trophic levels (t=-3.09, df=1, p=0.1992).

However, the dominant catchment cover did have a significant impact on the resources utilised. Biofilm was utilised within all environments. Forested cave streams utilised biofilm less than agricultural streams, both surface and cave, but were not different from forested surface streams (Fig. 3). FPOM also had different contributions to the community based upon the catchment type but not between caves and surface streams in the same catchment type (Tukey's HSD p <0.05, Fig.2). CPOM was exploited to the same degree regardless of cave presence or catchment type (Tukey's HSD p >0.05, Fig. 3).

Utilisation of resources by each taxon did not change across streams or between the cave and surface, except for one species (Mean diet compostition presented in Fig. 4). This suggests diets are similar across sites.
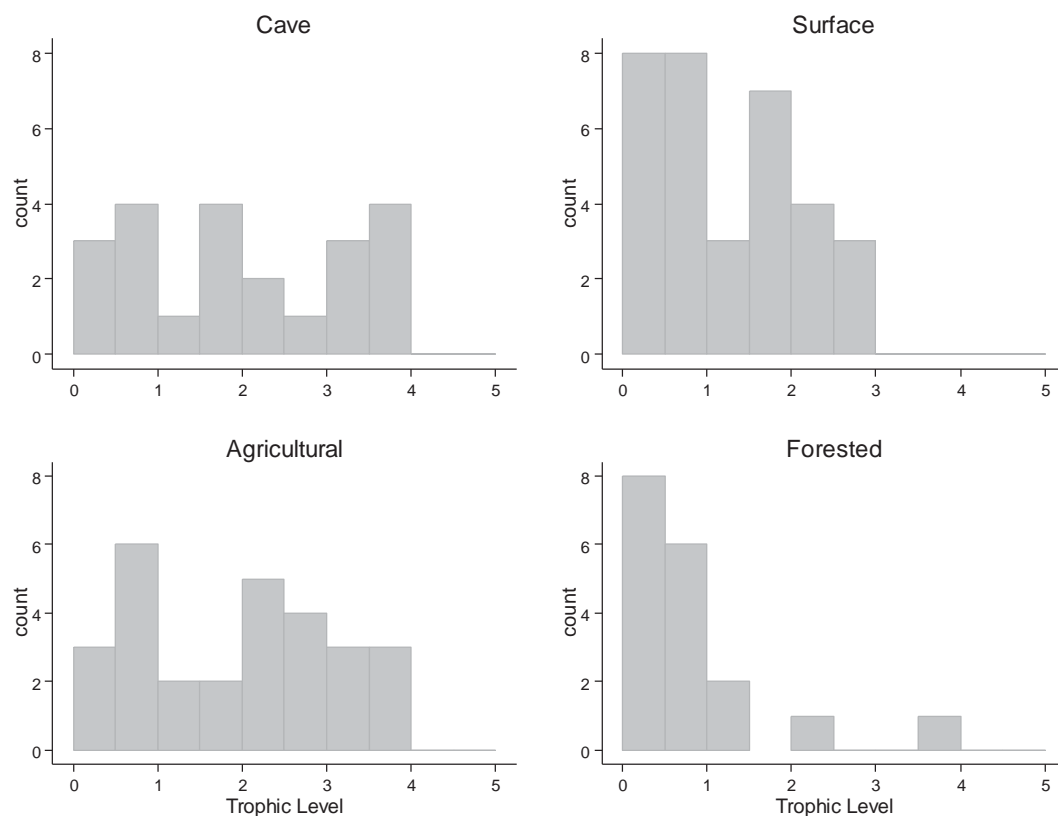
Figure 2: Number of species from each trophic level between cave and surface sites and forested and agricultural sites. Trophic levels as per (Vander Zanden et al., 1997).

Table 3: Results of t tests between community metrics based on stable isotope measures from data collected inside and outside of 4 caves in the Manawatū in 2014. df=3

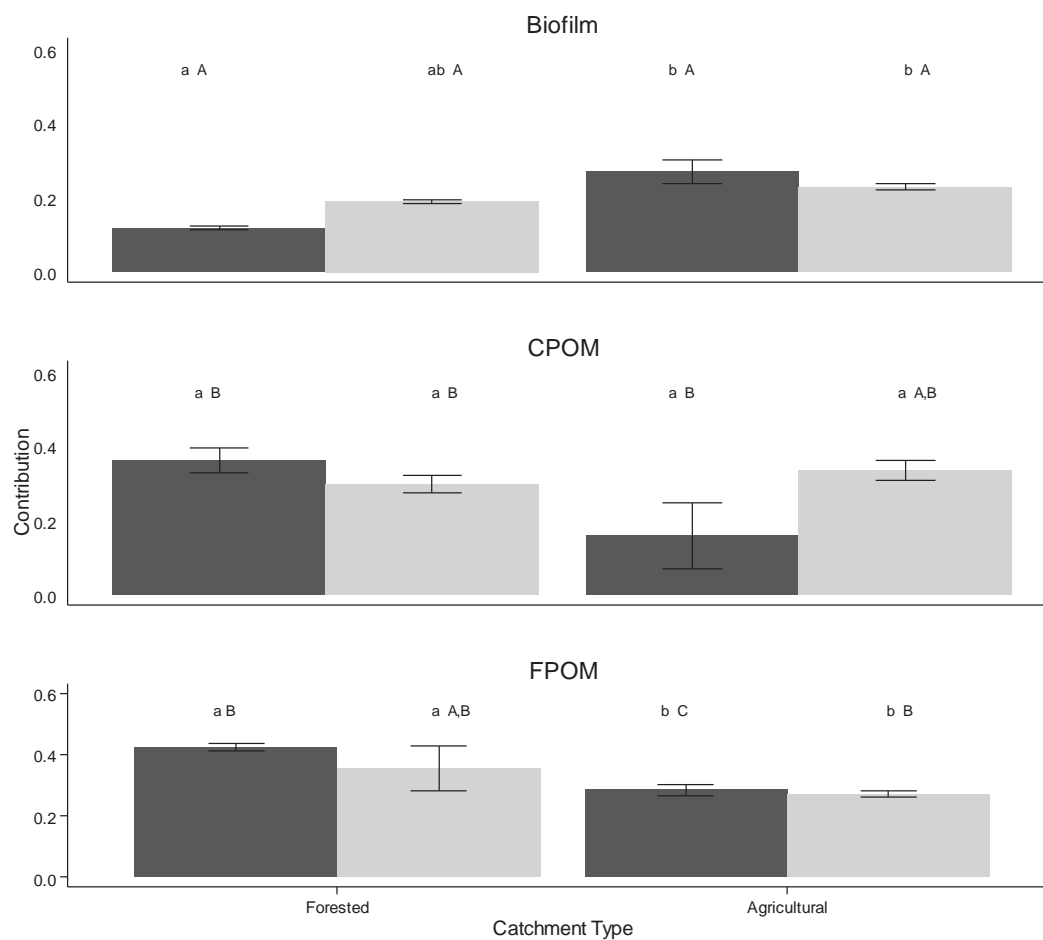| Metric	Cave/Surface		Dominant Catchment Cover	
	t	p	T	P
Nitrogen Range	-0.17	0.87	-1.7	0.19
Carbon Range	-0.21	0.85	1.98	0.14
Total Area	0.69	0.54	-0.38	0.73
Centroid Distance	-0.19	0.86	1.38	0.26
Nearest Neighbour Distance	-0.12	0.92	-0.39	0.72
SD of Nearest Neighbour Distance	-0.17	0.87	-0.18	0.87

Figure 3: Mean (± 1 SE) contribution of each resource to the overall community. Capital letters represent column differences. Lower case letters are the results of pairwise t tests. Different letters represent significant differences. Darker bars are cave sites, lighter are surface.
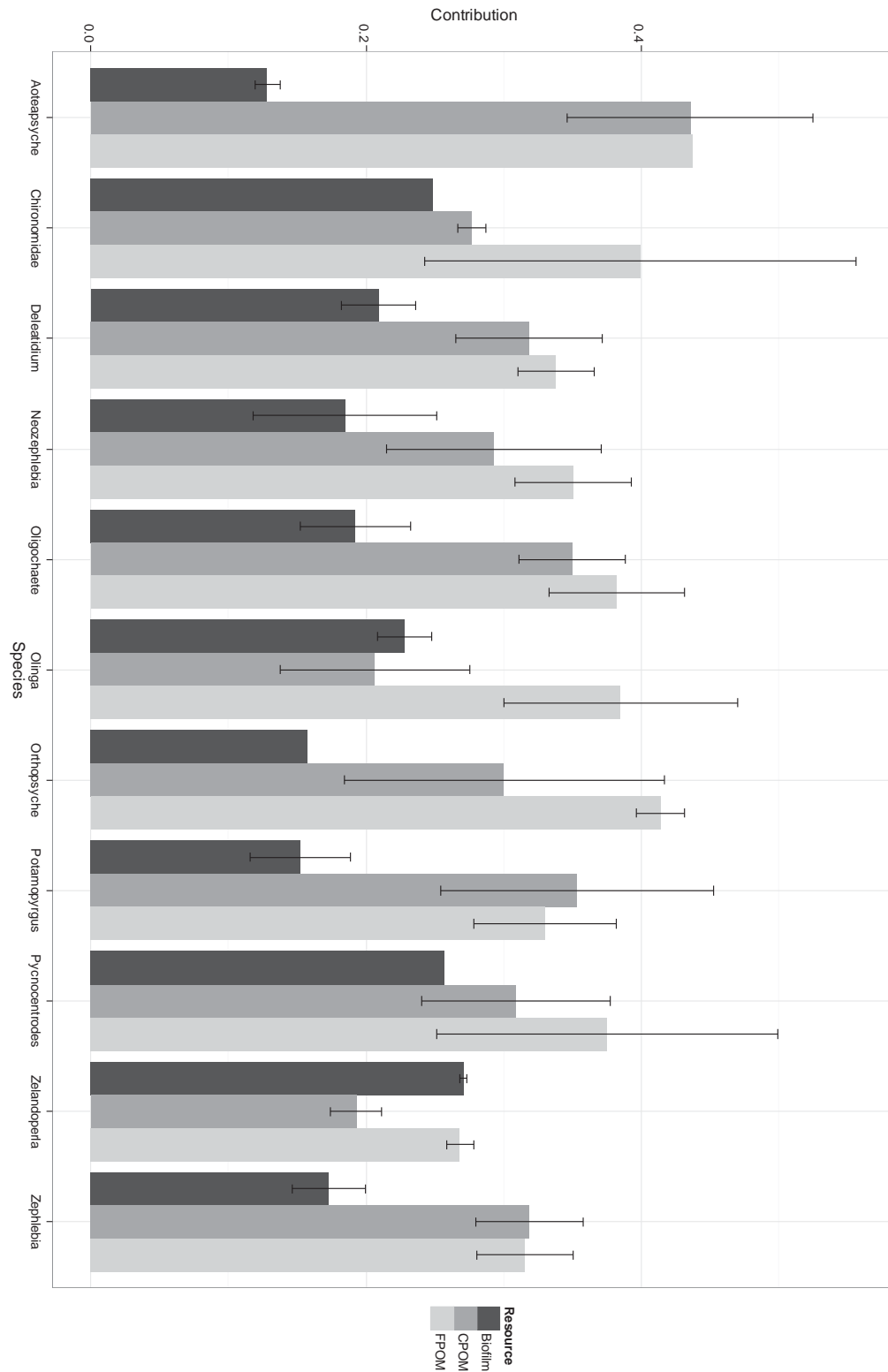
Figure 4 Mean (±1 SE) utilisation of resources by invertebrate species estimated through Bayesian

mixing models in SIAR(Parnell *et al.*, 2008). Where no error bars are present there was only one

value available for that species/resource pair.

Discussion

There was a difference in the resource utilisation patterns in streams draining agricultural catchments when compared to those in the forested catchments. But resource use did not differ between cave and surface streams draining the different catchment vegetation types. The communities had similar trophic structure as measured by isotope ratios both inside and outside the caves, and in the 4 different streams. The δ^{13}Carbon range was similar inside and outside the caves and across streams indicating that overall a similar number of resources were utilised within each community (Layman *et al.*, 2007). Trophic levels as per Vander Zanden *et al.* (1997) were the same for caves as for the surface, a conclusion supported by the similar δ^{15}N ranges (Layman *et al.*, 2007). Taxa appeared to have similar diets regardless of whether they were found in cave or surface communities or in forested or agricultural catchments.

Biofilm was a more important component of the agricultural food webs. Biofilms have also been found by others to be more important in agricultural streams compared to forest ones (Benstead and Pringle, 2004). Biofilm in agricultural caves seemed to constitute the most important resource for those communities, as it was used significantly more than other resources. Biofilm is known to be an important resource for cave environments, even where other resources are in abundance (Simon *et al.*, 2003), and so a reduction in other types of resources might increase the importance of biofilm to the community. The communities living in forested catchments seemed to use biofilm to a lesser degree than the agricultural stream communities. The role of biofilm in caves draining forested catchments was lower in comparison to the upstream surface streams. These caves had higher standing stocks of the other resources (i.e. CPOM and FPOM). The importance of biofilm to the communities is thus clearly related to the availability of alternative resources.

Differences in use of CPOM could not be detected between surface/cave or streams and catchment types. Although the weighted mean value of CPOM to agricultural caves was lower in comparison to all other sites, CPOM utilisation did not differ between cave and surface environments. Invertebrate shredders are one source of mass loss where connection to the surface occurs (Simon and Benfield, 2001). In the caves studied here, numbers of shredders were not important in determining differences in community structure (Chapter 2, this thesis), supporting the results found here of differences in CPOM not being important in determining the communities of these caves. However, Simon and Benfield (2001) also found that leaves within caves moved only short distances within caves before they were consumed and broken down (Simon and Benfield, 2001). It may be the case that at greater depths within these caves a difference in CPOM utilisation may be found, however, the present data do not suggest this. Thus, although it is likely the case that CPOM use by these cave communities is regulated by transportation distance and by the presence of surface sources, it remains an important source of nutrients and energy for communities in both forested and agricultural catchments.

FPOM was more important within forested catchments as a source of energy than for agricultural catchments. Though lower than for forested catchments, the role of FPOM in agricultural stream systems was high as a portion of the food consumed for these communities. FPOM is an important source of carbon entering food webs in caves (Simon *et al.*, 2003), and so it was expected to play an important role in the caves studied. Within the streams in this study, FPOM contributed between 27% and 43% of the energy to the communities assessed, and was the most consumed resource at forested sites. Fine particulate organic matter comprises a large part of the total energy consumed by stream invertebrates in New Zealand (Winterbourn *et al.*, 1981; Winterbourn *et al.*, 1984). This importance was carried below ground. FPOM remained a significant portion of the diet

within the caves, but no more important than on the surface (Fig. 2). As with New Zealand's surface streams, FPOM may play an important role in the communities below the surface.

The species with sufficient data to estimate dietary proportions across the study treatments indicated generalist feeding patterns. However, the types and proportions of food consumed did not change across catchment types or cave/surface. This may indicate that resource availability impacts the ability of different functional feeding groups to be competitive in that environment. This idea is supported by the fact that in these streams there is a difference in shredders that parallels the difference in resource use across catchments (Chapter 2). The use of stable isotopes for assessing diet proportions is a coarse method, however, it incorporates a temporal aspect and considers resource assimilation rather than just ingestion, thus providing a more reliable estimate of resource use (Rounick *et al.*, 1982; Benstead and Pringle, 2004). Rounick *et al.* (1982), using stable carbon isotopes, showed that invertebrates of the same species in New Zealand streams did differ in their dietary composition to some degree between forested and agricultural catchments. However, they do note that shredders were missing from catchments which had lost allochthonous inputs and their logged experimental catchments were still dependent on allochthonous energy (Rounick *et al.*, 1982). Thus, although New Zealand stream invertebrates are generalists, community structure can change following changes to resource inputs.

There was very little difference in the use of resources between cave and surface environments for all resources. Cave streams in agricultural catchments were very much like agricultural surface streams while forested caves were very much like forested surface streams. This result supports the view of a general dependence of caves on the surface environment for resource inputs (Culver and Pipan, 2009; Romero, 2009). Any change to resources in the surface streams will impact the subterranean biota and their feeding

relationships. The shift that was observed was from a stream where the majority of the energy entering into the community was terrestrially derived at the forested catchment sites to one wherein the energy was autochthonous, the agricultural streams. This is typical of most New Zealand streams draining different catchments (Rounick *et al.*, 1982; Gray *et al.*, 2011).

The alteration of stream food webs by agriculture has been observed before (Woodward and Hildrew, 2002; Benstead and Pringle, 2004). Agrochemicals used in high intensity farming systems, along with the deforestation of catchments, alter the availability of resources and the stoichiometry of the resource base. In turn this cascades through the food web (Hadley *et al.*, 1981; Woodward and Hildrew, 2002). In New Zealand, shifts to autochthonous energy sources for the bases of food webs of stream communities have been observed in response to the clear-cutting of forests (Rounick *et al.*, 1982). The shift in resource use was in response to the flushing of allochthonous resources and the removal of the canopy cover, two factors often associated with agriculture (Rounick *et al.*, 1982). Additionally, the change was associated with the loss of shredders from recently clear-cut streams which had an absence of litter material (Rounick *et al.*, 1982). Winterbourn *et al.* (1984) found that the dependence of stream food webs on autochthonous resources increased along a gradient of increasing light availability and riparian pasture. Internationally, Benstead and Pringle (2004) found through stable isotope analysis that one of the major threats to endemic fauna in Madagascar was the impact of native forest deforestation for conversion to agricultural land on the food webs of species. The differences in resource availability was responsible for the losses of endemic species within those streams (Benstead and Pringle, 2004). Similarly, the results here show a shift in the trophic bases of food webs between agricultural and forested catchments. In agreement with the present study Benstead and Pringle (2004) showed an increased importance of biofilm for agricultural catchments. This increased importance was true for agricultural

cave and surface streams in this study. Pollution events have also been observed to change community structure below ground. Evidence suggests that where organic pollution changes resource availability, the communities below are impacted (Simon and Buikema Jr, 1997; Wood *et al.*, 2008). For instance, organic pollution following a flooding event in 1999 at Peak Cavern cave in the UK was associated with no detection of any taxa for one month following the event and the abundance remaining lower than control sites for the next nine months (Wood *et al.*, 2008). Whether the impact is positive or negative depends on the intensity of the pollution, but generally results in decreased evenness and richness for cave communities (Holsinger, 1966; Simon and Buikema Jr, 1997; Wood *et al.*, 2002; Wood *et al.*, 2008).

The results presented here suggest that resource use in streams and caves in agricultural land are significantly different to those found under forested lands. This difference has impacts on the resource bases of the communities' trophic webs. The differences that are found on the surface are carried through to the caves. Thus, if the conservation of cave stream environments is to be a priority, the conservation of surface streams and the mitigation of the negative impacts of farming activities on these streams will need to be the first step.

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Chapter 4: General discussion

Waterfall at the exit of Piripiri cave.

The impact of land use on structuring cave stream invertebrate communities is a topic that has received little consideration. The link between the cave and surface environments has been well established and the dependence of the cave ecosystem on the surface for energy and nutrients is clear (Culver and Pipan, 2009; Romero, 2009). Furthermore pollutants from the surface can severely impact cave communities (Simon and Buikema Jr, 1997; Wood *et al.*, 2008). The effects of agriculture and its pollutants, alterations and inputs has however not been given much attention. This study examined the potential effects of agriculture in 4 small North Island cave streams.

The conclusion of my thesis was that these cave streams were less affected by agricultural land use than the corresponding surface streams. Community structure and biological indices (e.g. QMCI, EPT) all declined as the proportion of both the catchment and the riparian zone of the streams under agricultural use increased. This change also impacted the basal resources available for organisms and trophic pathways within the systems. Changes in community structure were most tightly linked with the amount of deposited sediment at a stream site. More sediment resulted in a more degraded community. However, the impact was reduced in comparison to the surface. The reduction in stream health and the community structure underground were overall less impacted when there was a greater degree of sedimentation.

The utilisation of resources was different between catchment types (i.e. agricultural and forested). Autochthonous production was more important for streams in agricultural catchments than for forested streams. However, allochthonous production was the main source of energy for the streams in all catchments. Interestingly, the importance of these different resources did not change for ecosystems inside the cave. The use of resources was related to the catchment type, possibly meaning that the dominant catchment cover alters the stream resource base, likely by regulating allochthonous inputs. Changes to the

resource base and greater levels of sediment in streams in agricultural land use altered caves community and trophic structure.

That sediment is one of the principal adverse effects of agriculture on subterranean stream ecosystems is consistent with the known impacts of agriculture land use on sedimentation of surface waterways (Ryan, 1991). Excessive sediment loading to streams is associated with lower habitat quality and food smothering for aquatic invertebrates (Ryan, 1991; Quinn and Stroud, 2002; Burdon *et al.*, 2013). This in turn reduces species richness, abundance, diversity and measures of health such as the QMCI or EPT indexes (Sarriquet *et al.*, 2007). The high sediment levels in agricultural streams flowed down into the cave, but less sediment was present in caves overall. As there are no additional inputs of sediment once water is inside the cave the surface sediment likely attenuates as it passes through the cave. Sediment transport within caves is known to be limited by the complexity of the passages and often only happens in appreciable amounts deep within caves during periods of high flow(White and White, 1968). Increased sediment deposition from agricultural streams is likely to be the most detrimental effect of land change on cave communities.

The results of chapter three suggest that differential resource availability also plays a role in the structuring of communities between catchment types. This difference is present between catchments both below and above ground. However, there is no difference in resource utilisation by communities above and below ground within the same catchment. This is likely due to the resource use in caves being regulated by the highly dependent link between the cave and surface environment (Romero, 2009). The resource use in agricultural catchments on the surface was more dependent on autochthonous production than the forested catchments. Interestingly, this was the case for cave streams in agricultural catchments as well, despite the lack of photosynthesis in those environments. This likely reflects a reduction in the availability of other resources in the environment

causing a shift in reliance to biofilms rather than of an increase in the production of biofilm in the cave streams under agriculture given what is known about changes in food webs under agricultural land use regimes. Cave communities are affected by sediment and resources from the surface that are in turn determined by land use.

Conclusion

Cave stream communities are impacted by agricultural practices on the surface. Similar factors affect both the cave and surface environments, although the cave communities are resistant to the changes observed on the surface. Sediment plays an important role in the structuring of the communities in streams draining agricultural catchments. It is likely that these impacts are similar to those experienced by surface communities, namely habitat and food smothering. That sediment smothers food may help to explain the difference in utilisation of resources by communities in streams draining agricultural catchments when compared to forested communities. However, the removal of allochthonous resources into streams also plays a role in altering the communities by conferring a greater utilisation of autochthonous biofilm resources by agricultural stream communities. Overall, it can be said that the effects of agriculture on cave environments in the Manawatū are negative, a reduction in QMCI (Stark, 1985), EPT family richness, and a community structure more similar to that of a degraded surface stream. However, the impacts are somewhat mitigated, likely reflective of the attenuation of sediment and the inability of macrophytes to dominate in an aphotic environment. By altering the habitat and diet of stream invertebrates, agriculture in the Manawatū is having a negative impact on the cave stream inhabitants. In these cave systems, cave ecosystem conservation will depend on remediation of the surface streams and reducing sediment loads entering the streams and caves through riparian planting.

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Whatungarongaro he tangata, toitū te whenua.

Men disappear, the land remains.