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**EFFECTS OF LAND-USE ON STRUCTURE  
AND FUNCTION OF AQUATIC  
INVERTEBRATE COMMUNITIES**



A thesis presented in partial  
fulfillment of the requirements  
for the degree of  
Master of Science in Ecology  
at Massey University

Christopher Leigh Guy

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## SUMMARY

Two aspects of benthic invertebrate community function; colonisation and resilience, were examined during January to March, 1996. In the first study (chapter 2) colonisation patterns of invertebrate communities were examined in 9 streams situated in 3 different land-use types in the Waikato region of New Zealand. The communities colonising tiles in streams situated in different land-use areas were found to be quite different. The communities of pasture streams had greater invertebrate abundance and taxonomic richness compared with forested sites and exotic *Pinus radiata* forest sites were more heavily dominated by a single taxa. Colonisation was found to proceed more quickly in streams located in pastoral catchments, followed by those in *Pinus radiata* and native podocarp / broadleaf forest. Two colonisation models (power and negative exponential) were fitted to the changes in community structure with no land-use differences being found. The greater and more quickly accruing periphyton levels found in the pasture streams, in providing a more food rich and structurally complex environment, may speed colonisation. Alternatively, land-use induced disturbance in the pasture and *Pinus radiata* catchments eliminating less resilient taxa and leaving better colonisers may explain why colonisation proceeds more quickly in these streams.

In the second study (chapter 3) structure and resilience of invertebrate communities inhabiting 4 streams in each of 3 different land-use categories; hill country pasture, *Pinus radiata* plantation forest and native podocarp / broadleaf forest, were examined in streams in the Waikato region of New Zealand. Community structure was assessed using detrended correspondence analysis to ordinate sites according to community composition. Community matrices were constructed and eigenvalues extracted to provide an estimate of community resilience. Although community composition was effected by land-use there was no corresponding effect on community resilience and nearly all the communities fell

outside the limits for local stability. Resilience appears to depend not on what particular taxa make up a community but on some threshold number being present to allow for normal community function.

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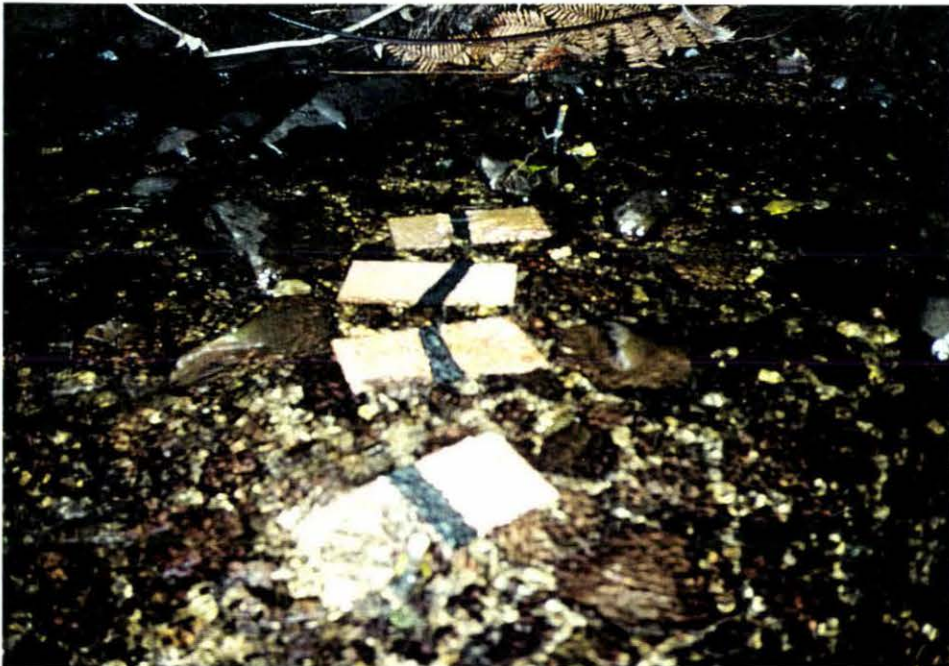
**Plate 1.** Pasture site PW2 at the AgResearch Station, Whatawhata.



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## **CHAPTER 1:**

### **GENERAL INTRODUCTION**

## GENERAL INTRODUCTION

Before the arrival in New Zealand of the first Polynesian settlers native forest covered 75% of the country's land area (Fahey and Rowe, 1992). Following two waves (Polynesian and European) of immigration and exploitation forest land has been reduced to 29% of the country's land area and consists of 6.4 million hectares of native forest and 1.4 million hectares of exotic production forest, of which 90% is *Pinus radiata* (New Zealand Official Yearbook, 1996). During this time 36% of New Zealand's land area has been developed as improved pasture (Rutherford *et al.*, 1987). A similar process has been evident in many countries worldwide (Townsend *et al.*, 1997).

Current thinking, stressing the importance of a catchment's landscape and vegetation to the characteristics of the stream draining it was aptly summarised by Hynes (1975) when he argued that "in every respect the valley rules the stream". Because of the dependence of a stream on its catchment, land-use changes such as native forest conversion to *Pinus radiata* forest and pasture have resulted in alterations to stream light, temperature and flow regimes, reduced water quality through sedimentation and eutrophication, changes to water pH and conductivity and changes in stream morphology (Cowie, 1985; Fahey and Rowe, 1992; Prat and Ward, 1994; Townsend *et al.*, 1997). Predictably, these disturbances have had a profound impact on the aquatic insect communities inhabiting the streams affected. A number of studies have reported land-use effects on measures of community structure such as taxonomic richness, diversity, abundance and composition (Allen, 1959; Winterbourn, 1986; Quinn and Hickey, 1990; Reed *et al.*, 1994; Richards and Host, 1994; Townsend *et al.*, 1997). Although land-use impacts on aquatic invertebrate community structure are well documented how these changes in structure impact on community function is less clear. Community function includes such community processes and attributes as food processing, colonisation, nutrient cycling and resilience.

Benthic invertebrates appear to have a low resistance to disturbance e.g., large declines in abundance and diversity have been reported in response to disturbances (Sagar, 1986), however, these communities remain persistent over longer time periods (Townsend *et al.*, 1987; Death and Winterbourn, 1994). This persistence is maintained by the communities ability to recover rapidly following disturbance i.e., they have a high resilience. Resilience is a measure of how quickly communities recover from disturbance (Begon *et al.*, 1990), while colonisation is the primary mode of recovery following disturbance (Sheldon, 1984). Drift (Townsend and Hildrew, 1976; Williams and Hynes, 1976) and the build-up of periphyton and organic detritus on the substrates being colonised (Roby *et al.*, 1978; Meier *et al.*, 1979; Mathooko, 1995) are reported to be major influences on colonisation, while resilience is held to be dependent on the complexity of the particular community studied (MacArthur, 1955; Elton, 1958; Gardener and Ashby, 1970; May, 1972, 1973).

This study considers the effect of three land-use types; hill country pasture, exotic *Pinus radiata* production forest and native broadleaf / podocarp forest, on aquatic invertebrate communities. Community structure is examined to establish whether it is affected by land-use as predicted by the literature, and, if this is the case, the effect of changed community structure on two aspects of community function, colonisation and resilience, is examined.

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## **CHAPTER 2:**

# **THE EFFECT OF LAND-USE ON LOTIC INVERTEBRATE COLONISATION PATTERNS.**

## THE EFFECT OF LAND-USE ON LOTIC INVERTEBRATE COLONISATION PATTERNS.

### ABSTRACT

Colonisation patterns of invertebrate communities were examined in 9 streams situated in 3 different land-use types in the Waikato region of New Zealand. The communities colonising tiles in streams situated in different land-use areas were found to be quite different. The communities of pasture streams had greater invertebrate abundance and taxonomic richness compared with native podocarp / broadleaf and exotic *Pinus radiata* forest sites and the pine forest sites were more heavily dominated by a single taxa. Colonisation was found to proceed more quickly in streams located in pastoral catchments, followed by those in *Pinus radiata* and native podocarp / broadleaf forest. Two colonisation models (power and negative exponential) were fitted to the changes in community structure with no land-use differences being found. The greater and more quickly accruing periphyton levels found in the pasture streams, in providing a more food rich and structurally complex environment, may speed colonisation. Alternatively, land-use induced disturbance in the pasture and *Pinus radiata* catchments eliminating less resilient taxa and leaving better colonisers may explain why colonisation proceeds more quickly in these streams.

**Keywords;** Land-use; disturbance; macroinvertebrates; community structure; colonisation patterns; colonisation models; drift; periphyton.

## INTRODUCTION

The importance of the catchment to its stream has been immortalised by Hynes' (1975) now classic statement "in every respect, the valley rules the stream". The dependence of a water body on the character of its catchment is also a vital part of many paradigms in aquatic ecology such as the river continuum concept (Vannote *et al.*, 1980). A stream's hydrology, water chemistry, nutrient inputs and light levels are all determined by the geology, climate and vegetation of its catchment (Allan and Johnson, 1997; Allan *et al.*, 1997; Townsend *et al.*, 1997). In turn, human activities which alter catchment conditions (usually involving alteration of catchment vegetation) can greatly impact on streams. Furthermore, land-use impacts are becoming increasingly important relative to other catchment influences as drainage basins are more intensively developed.

Although flow events (e.g. spates and prolonged low flow) are obvious sources of disturbance in streams, anthropogenic factors such as land-use modification may also act as disturbances (Resh *et al.*, 1988). Disturbance, from changes in flow, is widely regarded as a major determinant of lotic community structure (Resh *et al.*, 1988; Townsend, 1989; Poff, 1992) and has been demonstrated to effect periphyton abundance and composition, invertebrate taxonomic richness, abundance, diversity, and functional feeding group composition (Hemphill and Cooper, 1983; Gurtz and Wallace, 1984; Robinson and Minshall, 1986; Death and Winterbourn, 1995; Townsend *et al.*, 1997).

Catchment modification, however, is also a form of disturbance which can alter a number of stream characteristics including; reductions in water quality through sedimentation and eutrophication, altered light, temperature, and flow regimes, changes to water conductivity, pH, and nutrient levels, altered stream morphology, changes to the nature, and quantity of nutrient inputs and the particle size distribution, and stability of the substrate (Cowie, 1985; Winterbourn, 1985; Fahey and Rowe, 1992; Prat and Ward, 1994; Quinn *et al.*, 1994; Townsend *et al.*,

1997). In turn, these land-use effects are recognised as having a major impact on invertebrate communities (Winterbourn, 1985, 1986; Smith *et. al.*, 1993; Quinn *et. al.*, 1994).

The exact manner in which disturbance affects benthic invertebrate diversity in streams is largely unresolved (Death and Winterbourn, 1995), however, understanding colonisation is integral to understanding the effects disturbance at a community level. "Colonisation can be viewed as the sequence of events that leads to the establishment of individuals, populations,.....(*or communities*) in places from which they were..... absent" (Sheldon, 1984). Although over small time scales species abundance and diversity may undergo fluctuations caused by disturbances, over larger spatio-temporal scales aquatic insect communities are relatively persistent (Townsend *et. al.*, 1987; Richards and Minshall, 1992; Death and Winterbourn, 1994). This persistence is maintained largely through the ability of invertebrate communities to recover quickly from perturbations i.e., they show a high resilience (Mackay, 1992). Colonisation is the primary mode of recovery following disturbance; the alternative being persistence in dormant, resistant life stages (Sheldon, 1984). Colonists come from a variety of sources. Drifting individuals may be the major source, with direct oviposition, movement from the hyporheic zone and adjacent areas of substratum also contributing (Williams and Hynes, 1976).

While many experimental studies have described colonisation in lotic systems (e.g., Sheldon, 1977; Meier *et. al.*, 1979; Gore, 1982; Lake and Doeg, 1985; Mathooko, 1995) and related this to instream phenomena such as drift (Waters, 1964; Townsend and Hildrew, 1976; Williams and Hynes, 1976; Mathooko and Mavuti, 1992) and hydrologic disturbance (Malmqvist and Otto, 1987), few have examined the impact of surrounding catchment land-use on colonisation. In this study I examine the colonisation dynamics of invertebrate communities in streams of three different land-use types; hill country pasture, exotic pine forest and native broadleaf / podocarp forest.

## STUDY SITES

The 9 streams in this study are located in 3 land-use categories; hill country pasture (PW2, PW3 and PW5), *Pinus radiata* plantation (EM1, EM2 and ES) and native broadleaf / podocarp forest (NF, NKL and NW5), along 13 km of the Hakarimata Ranges, west of Hamilton, New Zealand ( $175^{\circ} 15' \text{E}$ ;  $37^{\circ} 47' \text{S}$ ). The streams are small, (third order or less) with the largest less than 3.5 m wide. The catchments of the study reaches are also correspondingly small, with most smaller than 3 km<sup>2</sup> (Smith *et. al.*, 1993) and with the exception of site ES, all are composed entirely of a single land-use category. ES is estimated to be 79% *Pinus radiata* and 21% native broadleaf / podocarp forest (Quinn *et. al.*, 1994). The catchments above the study reaches are dominated by steep ( $>30^{\circ}$ ) to hilly topography (Smith *et. al.*, 1993) and the site elevation ranges from 35 m to 120 m above sea level (Quinn *et. al.*, 1994).

The pasture streams drain catchments cleared of native forest cover for approximately 60 yrs (Quinn *et. al.*, 1994) and are currently managed for sheep and beef farming. These streams typically have narrow, deep channels and although accessible to stock appear relatively stable. Substrate consists of a mixture of silt and gravel with many larger cobbles. Periphyton and macrophyte growth is prolific during late summer at these sites. Also converted to pasture 60 yrs ago, the pine forest catchments were reforested with *Pinus radiata* 17 yrs ago as part of the Ngaruawahia State Forest (Quinn *et. al.*, 1994). These streams are physically unstable with considerable scouring and slumping of the banks, and turbid water. Few large stones are present in these streams with the substrate dominated by fine gravel, silt and woody detritus. Site ES, however, was an exception having a substrate more typical of the native streams in the study (i.e. more stable and less dominated by fine particles). The native broadleaf / podocarp forest is drained by streams of a wider and shallower profile than those in the other land-use areas. Although having predominately gravel substrates, large stones and patches of bedrock are common in these streams. Site characteristics are recorded in table 1.

**Table 1:** Physico-chemical characteristics of the 9 study reaches. The upper part of the table contains data taken from surveys conducted November 1992 - March 1993 (Smith *et. al.*, 1993; Quinn *et. al.*, 1994) while the lower portion (in italics) contains recordings taken between 26 January and 9 March 1996. \*Catchment is estimated to be 79% *Pinus radiata* and 21% native broadleaf / podocarp forest (Quinn *et. al.*, 1994). # Thermometers from these sites were lost between day 7 and 21.

Site code	PW2	PW3	PW5	EM1	EM2	ES	NF	NKL	NW5
Land-use	pasture	pasture	pasture	pine	pine	pine*	native	native	native
Site elev. (m)	90	100	60	50	35	55	40	120	70
Catchment area (km <sup>2</sup> )	0.95	0.49	2.59	0.88	1.31	0.69	2.01	0.525	3.00
Mean temp. (C <sup>o</sup> )	13.2	16.3	14.2	13.5	13.6	12.5	12.5	12.2	12.2
Max. temp. (C <sup>o</sup> )	15.8	22.7	17.4	15.4	15.7	14.7	15.2	13.6	14.6
Min. temp. (C <sup>o</sup> )	11.0	12.7	11.3	12.0	12.0	10.0	10.0	10.3	10.1
Mean flow (L/s)	16	7	45	11	17	8	32	10	55
pH	7.50	7.40	7.48	7.06	7.20	7.53	7.62	7.38	7.56
E.C. (us/cm)	108.5	88.3	107.1	90.4	100.0	96.4	122.9	116.4	122.2
Turbidity (FTU)	6.0	7.6	5.3	21.3	23.5	12.0	4.1	6.7	4.4
<i>Mean temp. (C<sup>o</sup>)</i>	19.2	19.5 <sup>#</sup>	18.6	16.1	16.0	15.0	15.1 <sup>#</sup>	14.0	14.9
<i>Max. temp. (C<sup>o</sup>)</i>	27.0	26.0 <sup>#</sup>	24.0	19.0	18.5	17.5	17.0 <sup>#</sup>	17.0	18.0
<i>Min. temp. (C<sup>o</sup>)</i>	14.0	14.5 <sup>#</sup>	15.0	13.0	14.0	11.0	14.0 <sup>#</sup>	12.0	12.0
<i>Mean velocity (m/s)</i>	0.131	0.101	0.282	0.128	0.113	0.120	0.201	0.085	0.138
<i>Stream depth (m)</i>	0.070	0.049	0.062	0.044	0.063	0.056	0.050	0.051	0.048
<i>Stream width (m)</i>	1.09	1.05	1.26	0.93	1.14	1.96	1.24	1.41	3.32

## METHODS

### Colonisation experiment

Twenty terracotta tiles (manufactured by Revestimentos Ceramics, Apartado Aereo 27540, Bogota, Colombia) were placed in 5 rows of 4 in riffles at each study reach. The tiles measured 0.21 x 0.11 x 0.01 m (0.05 m<sup>2</sup>) and were secured by looping a strap of motorcycle tyre inner tube around each tile and wiring them to pegs driven into the stream bed.

All tiles were put out on January 25 or 27, 1996. Four randomly selected tiles were removed after 1, 4, 7, 21 and 42 days, the trial concluding on March 7 or 9, 1996 respectively. Each tile was sampled by lifting it quickly into a 250 µm net.

Periphyton was sampled, as described below, before the invertebrates were removed from the tile using a scrubbing brush and preserved in 70% isopropyl alcohol. Macroinvertebrates were identified and enumerated to the lowest possible taxonomic group using available keys. Taxa not able to be identified were assigned to apparent morphospecies.

A 6.16 cm<sup>2</sup> circular area of periphyton was sampled from each tile using a 2.8 cm diameter scouring disc (Davies and Gee, 1993). Four periphyton samples were also taken from the undisturbed substrate at each site at the beginning and end of the colonisation period. Each sample was stored on ice in the field and frozen before pigment extraction in 90% acetone overnight. Concentrations of chlorophyll a and pheophytin a were determined following Moss (1967a, b).

At all 9 sites faunal drift was sampled at the beginning and end of the colonisation period. A drift net (5.5 x 10 cm aperture; 0.5 mm mesh net) was set upstream of the riffle in which the tiles were located and left in place for 24 hours. Invertebrates were removed and preserved in 70% isopropyl alcohol.

At each site, 15 stones, in 3 different size categories (maximum linear, planar dimension 91-180 mm, 60-90 mm, and <60 mm) were sampled for invertebrates at the termination of the colonisation period. Stones were lifted into a 250 µm net and the invertebrates removed with a scrubbing brush before being preserved in 70% isopropyl alcohol. Macroinvertebrate numbers were normalised to tile surface area by calculating invertebrate numbers per unit surface area of stone (stone surface area = 1.15 x (width x breadth + length x breadth + length x width)). Number of taxa on the stones with a surface area closest to that of the tiles was averaged to provide an estimate of taxonomic richness.

### Statistical analysis

A power function

$$N_t = at^b$$

and a negative exponential function

$$N_t = k/m(1 - e^{-mt})$$

were tested for their ability to describe changes in a number of community characteristics.

SOLO (Hintze, 1988) was used to fit the functions to data for;

- (1) Taxonomic richness (S)
- (2) Abundance (N)
- (3) Margalef's index (Clifford and Stephenson, 1975), a simple measure of diversity given by:

$$D = (S-1) / \ln N$$

(4) The Berger-Parker index (Berger and Parker, 1970), a simple measure of evenness given by:

$$E = N_{\max} / N$$

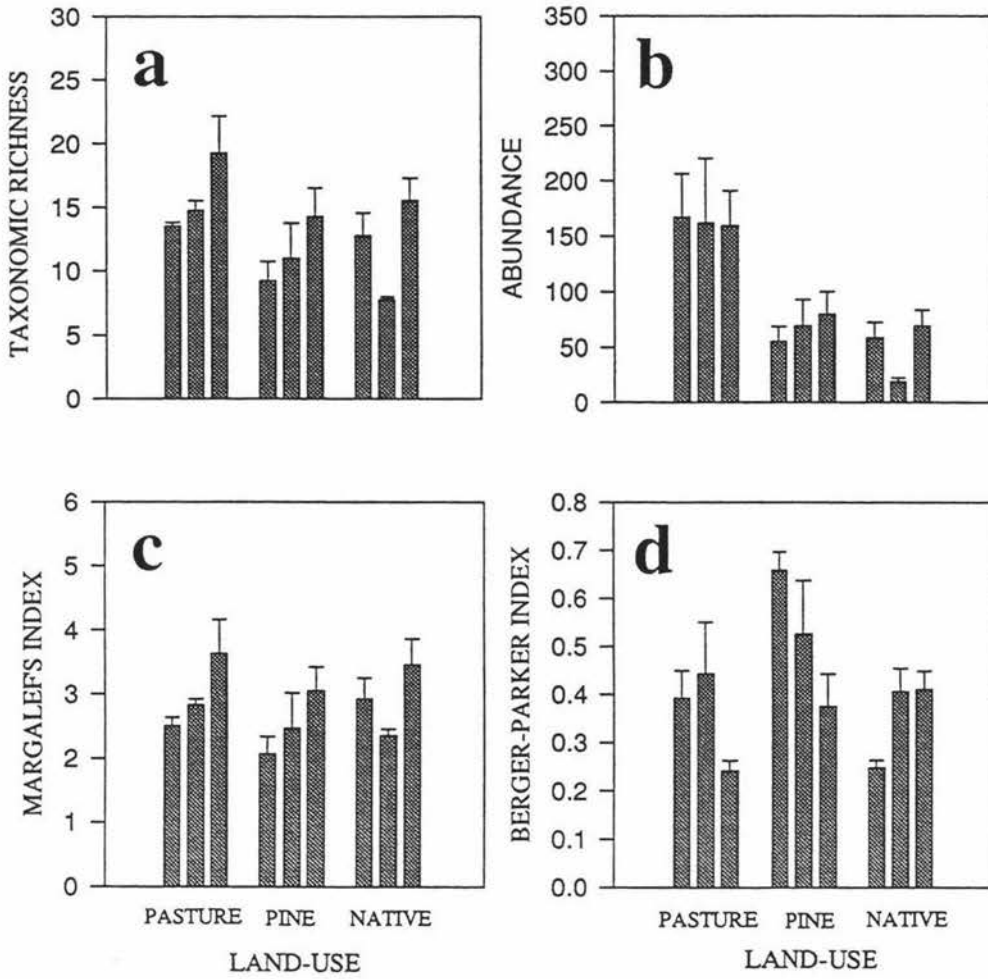
where  $N_{\max}$  = the number of individuals of the numerically dominant taxa.

Goodness of fit was tested using SYSTAT (1996) following Bates and Watts (1988). Tile communities were compared with respect to land-use with a two-way ANOVA using the GLM procedure of SAS (1989) and time to "completed colonisation" assessed as no significant ( $P > 0.05$ ) difference from those structural characteristics measured for the communities of the undisturbed substrate.

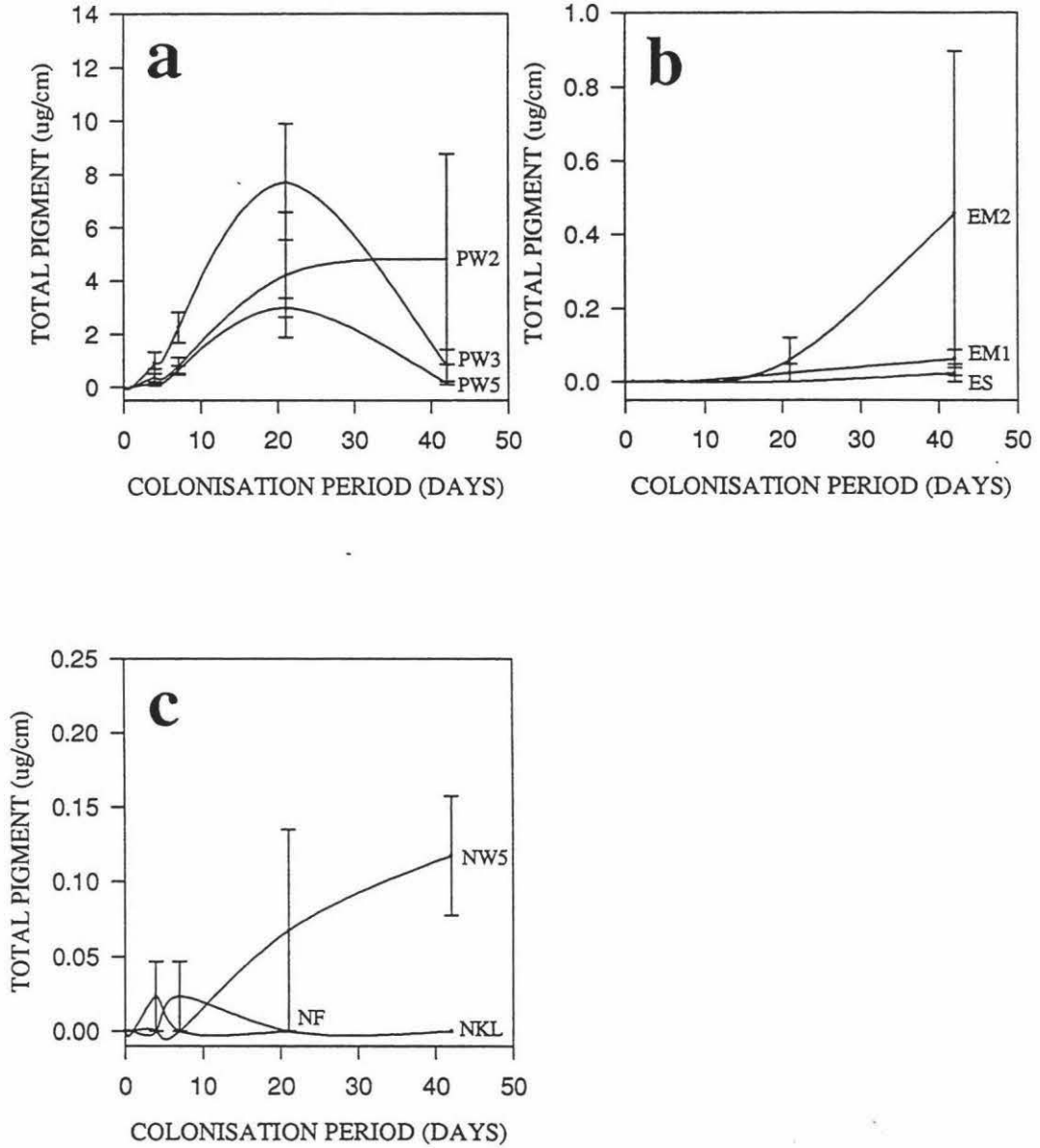
## RESULTS

### Community structure

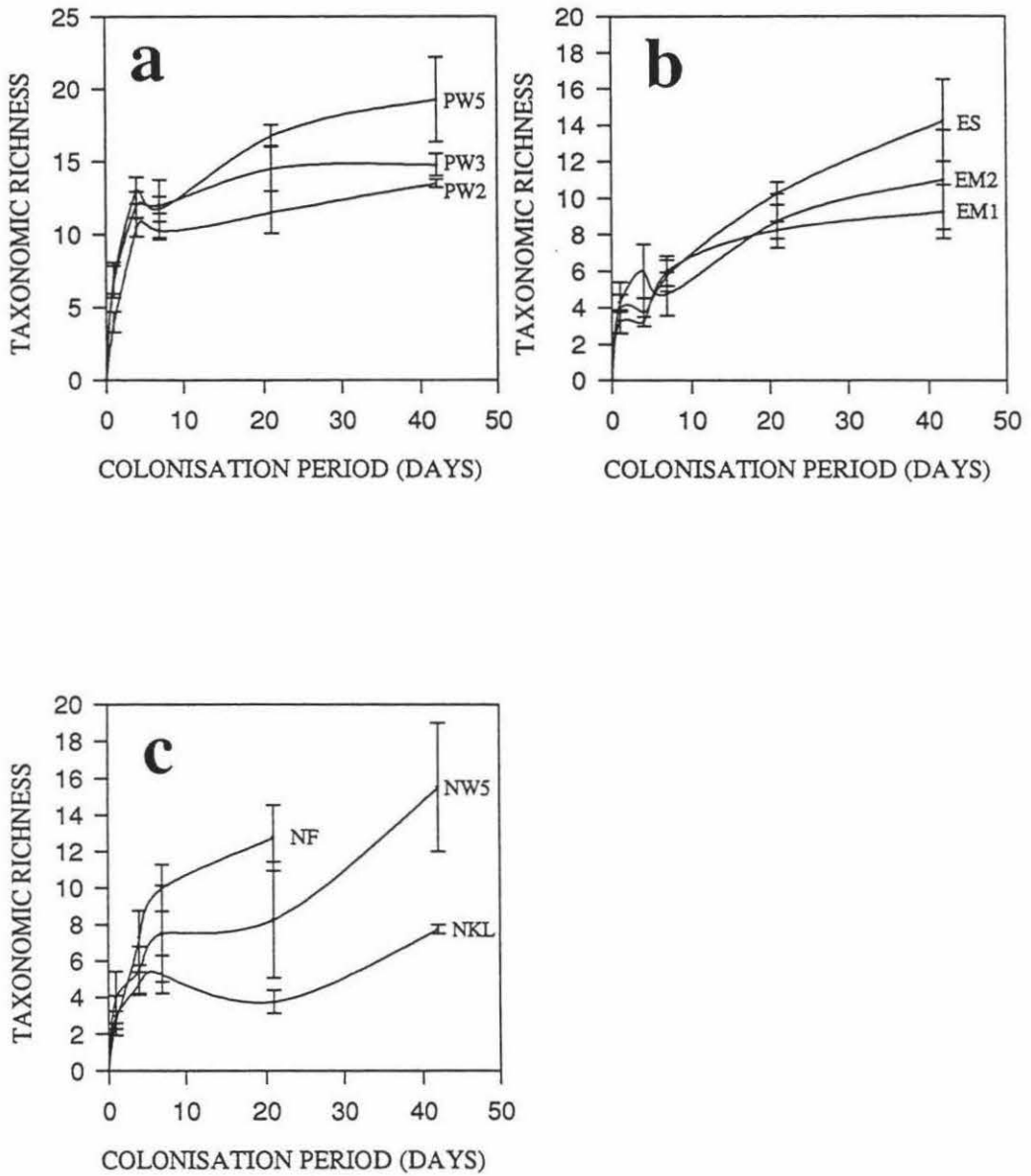
The communities colonising tiles at the pasture sites had a relatively even spread of individuals in 8 taxonomic groups while the forest communities were dominated by Ephemeroptera which accounted for 35 to 75% and 70 to 95% of the individuals in native and pine sites respectively. Sites in pasture tended to be numerically dominated by Mollusca, Diptera and Trichoptera, but with other groups also making sizeable contributions. At the end of the colonisation period taxonomic richness was significantly higher in the pasture streams than in either the native or pine forest streams ( $F_{2,27} = 10.58$ ,  $P < 0.001$ ), (Fig. 1). However, within each land-use category there was also a significant difference between individual streams ( $F_{6,27} = 2.62$ ,  $P = 0.04$ ). Total abundance was also significantly different ( $F_{2,27} = 28.28$ ,  $P < 0.001$ ) between all land-use types, with tiles in pasture sites attracting the greatest abundance of individuals followed by those in pine and native forest. Interestingly, when diversity was evaluated, accounting for these differences in



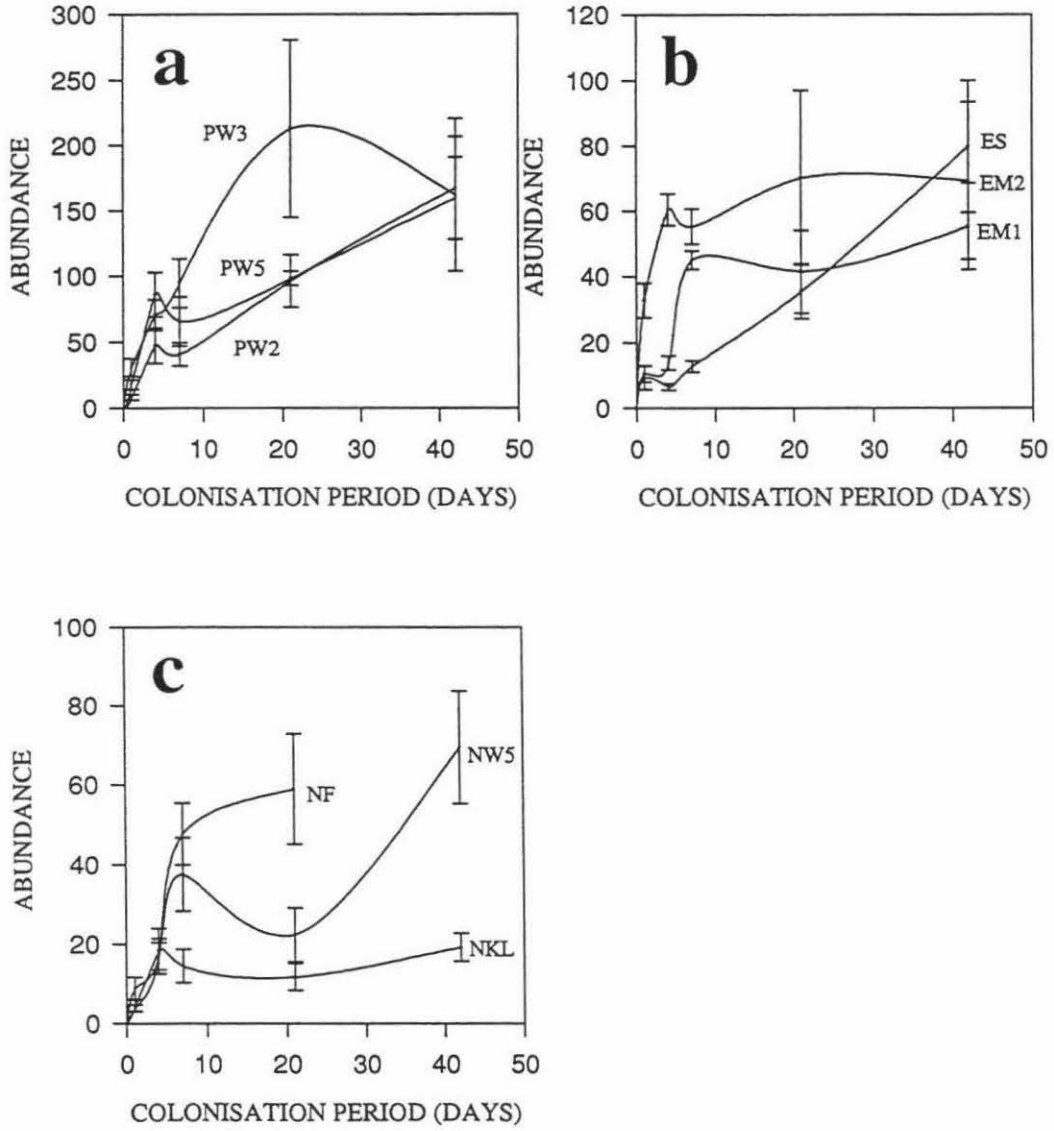
**Figure 1:** Mean ( $\pm 1$  S.E.) (a) taxonomic richness, (b) total abundance, (c) Margalef's Index and (d) Berger-Parker Index, for invertebrate assemblages on tiles collected on completion of 42 day colonisation in 9 Waikato streams differing in land-use.



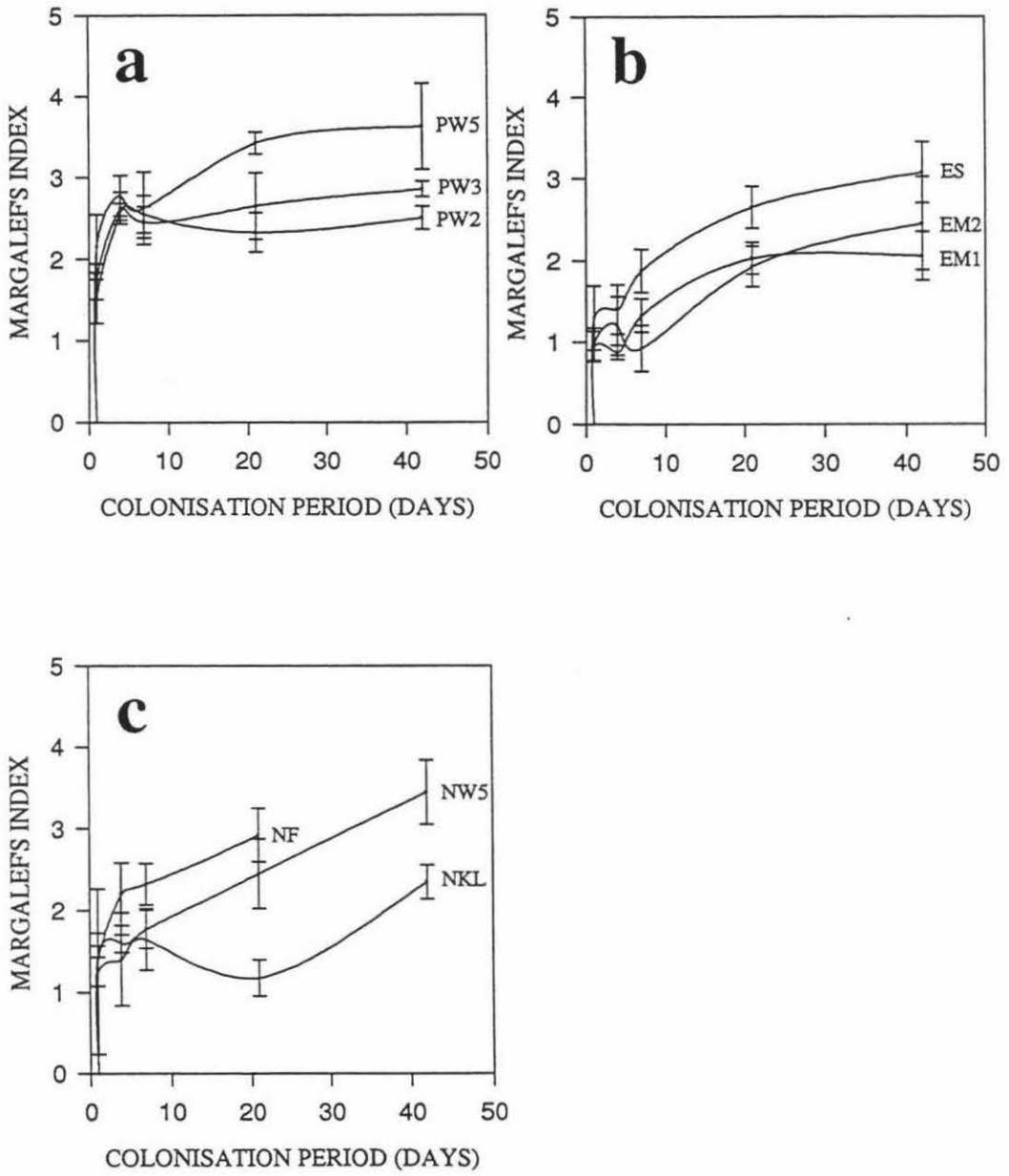
**Figure 2:** Mean total pigment (chlorophyll *a* + pheophytin *a*), ( $\pm 1$  S.E.) collected from tiles on day 1, 4, 7, 21 and 42, in three streams in each of three land-use types: (a) hill country pasture, (b) *Pinus radiata* plantation forest, (c) native broadleaf / podocarp forest.



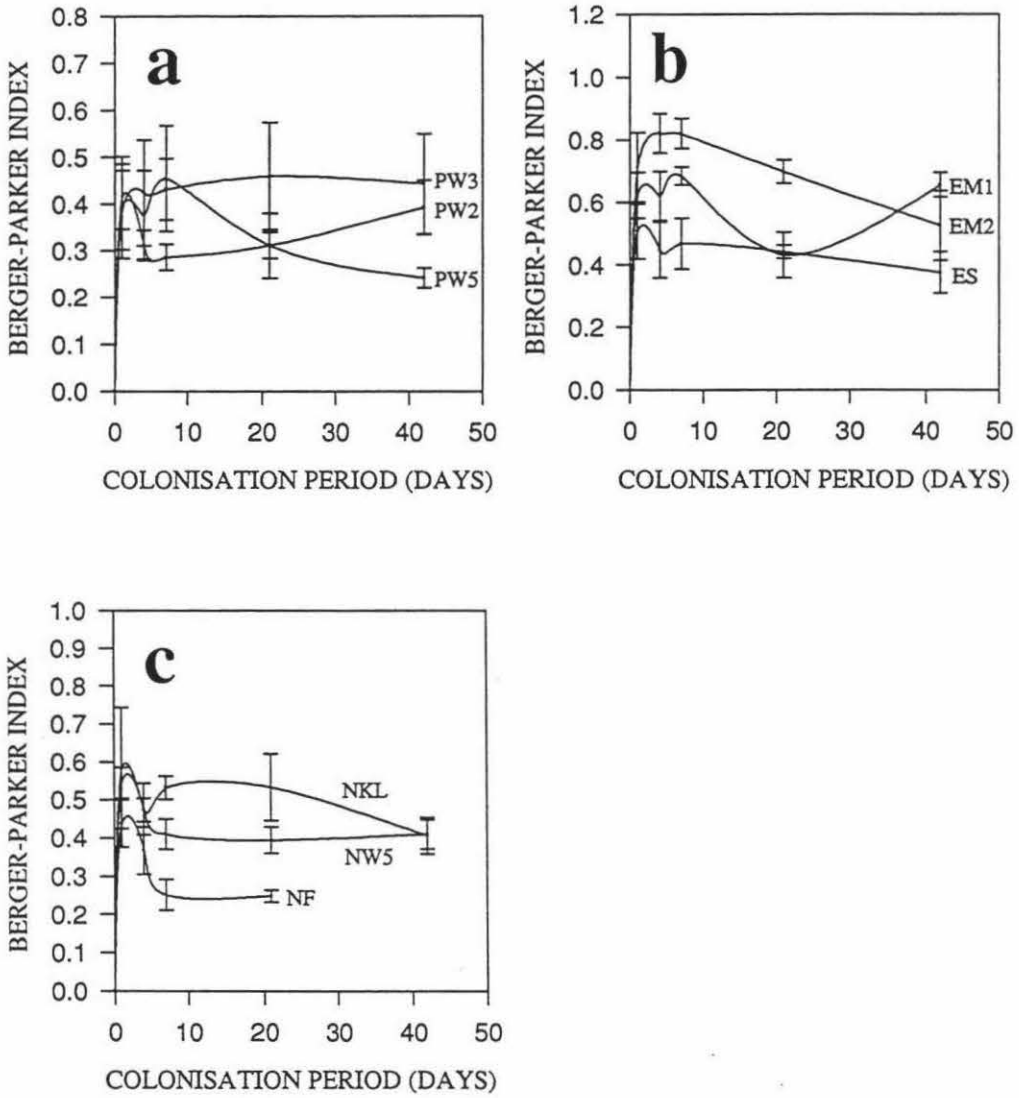
**Figure 3:** Mean taxonomic richness ( $\pm 1$  S.E.) for invertebrate assemblages collected from tiles on day 1, 4, 7, 21 and 42, in three streams in each of three land-use types: (a) hill country pasture, (b) *Pinus radiata* plantation forest, (c) native broadleaf / podocarp forest.



**Figure 4:** Mean abundance ( $\pm 1$  S.E.) for invertebrate assemblages collected from tiles on day 1, 4, 7, 21 and 42, in three streams in each of three land-use types: (a) hill country pasture, (b) *Pinus radiata* plantation forest, (c) native broadleaf / podocarp forest.



**Figure 5:** Mean Margalef's Index ( $\pm 1$  S.E.) for invertebrate assemblages collected from tiles on day 1, 4, 7, 21 and 42, in three streams in each of three land-use types: (a) hill country pasture, (b) *Pinus radiata* plantation forest, (c) native broadleaf / podocarp forest.



**Figure 6:** Mean Berger-Parker Index ( $\pm 1$  S.E.) for invertebrate assemblages collected from tiles on day 1, 4, 7, 21 and 42, in three streams in each of three land-use types: (a) hill country pasture, (b) *Pinus radiata* plantation forest, (c) native broadleaf / podocarp forest.

abundance using Margalef's index there was no significant difference between land-use type ( $F_{2,27} = 1.89$ ,  $P = 0.17$ ). Streams in pine forest had communities most heavily dominated by a single taxon ( $F_{2,27} = 6.25$ ,  $P = 0.01$ ), which, in all cases, was *Zephlebia dentata*, although, again individual streams differed within each land-use category ( $F_{6,27} = 3.07$ ,  $P = 0.02$ ).

### Periphyton

Pigment concentrations were at least an order of magnitude greater on tiles at pasture sites than those at forest sites until day 42 when periphyton biomass at 2 of the 3 pasture sites decreased after the initial peaks (Fig. 2). The pine sites exhibited a steady increase in periphyton biomass up to the end of the colonisation period and periphyton levels at the native sites were consistently low. Periphyton levels on the tiles in all 9 streams were not significantly different from those of the surrounding substrate after only 1 day (Table 2).

### Colonisation patterns

Taxonomic richness of the tile communities was higher at the pasture sites compared to the forest sites over most of the colonisation period (Fig. 3). Differences were also apparent in the shape of the curves with respect to land-use. Increase in taxonomic richness at the pasture and pine forest sites appeared to level off as colonisation proceeded, whereas the native forest sites exhibited continual increase. Taxonomic richness of the tiles was not significantly different from that of a tile sized area of undisturbed substrate ("completion of colonisation") in 4 days at the pasture sites, in 21 days at the pine forest sites and between 4 and 42 days at the native forest sites (Table 2). Abundance of individuals on tiles was also higher in the pasture sites over most of the colonisation period with the difference increasing as colonisation proceeded (Fig. 4). In contrast to taxonomic richness, increase in total abundance did not appear to slow as colonisation proceeded, with the exception of two pine forest (EM1 and EM2) and one pasture site (PW3), which appeared to plateau out around day 25. Macroinvertebrate abundance

**Table 2:** Time for macroinvertebrate and periphyton levels on tiles at the 9 study sites between January 25 and March 9, 1996 to approach that of the substrate. Values quoted give time in days before the taxonomic richness, abundance and periphyton (total pigment ( $\mu\text{g} / \text{cm}$ ) do not differ significantly ( $P > 0.05$ ) from those of the undisturbed substrate. In all cases d.f. = 19, 29 and 22 for taxonomic richness, abundance and periphyton respectively, except for site NF where d.f. = 16, 26 and 19 respectively.

Site code	Taxonomic richness	Abundance	Periphyton
<b>Pasture</b>			
PW2	4	1	1
PW3	4	1	1
PW5	4	4	1
<b>Pine</b>			
EM1	21	1	1
EM2	21	4	1
ES	21	21	1
<b>Native</b>			
NF	4	1	1
NKL	42	> 42	1
NW5	7	7	1

on the tiles was not significantly different from that of a tile sized area of undisturbed substrate (“completion of colonisation”) in just 1 or 4 days at the pasture sites (Table 2). This varied between 1 and 21 days at the pine sites and between 1 and more than 42 days at the native sites.

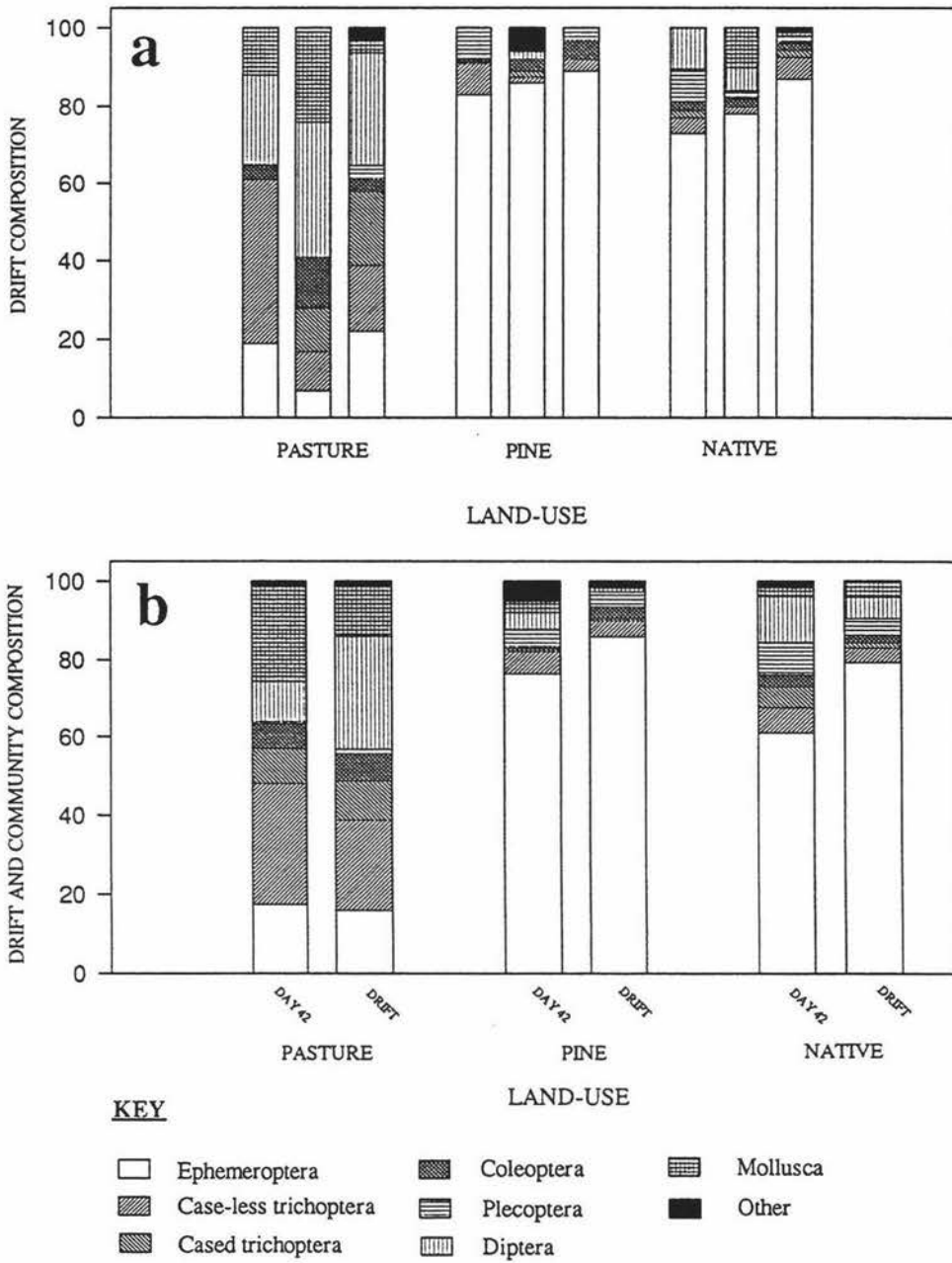
Changes in Margalef’s index over the colonisation period were similar to those for taxonomic richness (Fig. 5). Diversity was higher at the pasture sites compared to the forest sites over most of the colonisation period. While diversity at the pasture and pine sites levelled off over the exposure period, the native sites showed no indication of plateauing out. Dominance (Berger-Parker index) did not show strong patterns with respect to land-use type (Fig. 6). In general dominance decreased as colonisation progressed and streams in forest, especially pine, had higher Berger-Parker index values.

## Colonisation models

Both power and negative exponential curves were fitted to the changes in community structure (taxonomic richness, abundance, Margalef's index and the Berger-Parker index) over the 42 day colonisation period (Table 3). Colonisation patterns of taxonomic richness were modelled best by the power function in all the pasture and pine streams, with the exception of PW2, for which the negative exponential was a better fit. Taxonomic richness of the native forest streams showed no distinct model fit with fits to the negative exponential, power function and neither model for NF, NW5 and NKL, respectively. The negative exponential function modelled changes in abundance of individuals at all sites except PW2, PW3, and NW5, while Margalef's index was modelled best by the power function in all the forest streams, but only one pasture site. No discernible trend was observed for the Berger-Parker index with only one instance of either function fitting the data.

## Drift

A total of 202 individuals, comprising 30 taxa, were obtained in drift collections from pasture sites, while 218 individuals from 31 taxa and 188 from 20 taxa were collected in native and pine streams respectively (Fig. 7a). Drift at all forest sites was dominated by Ephemeropterans (particularly *Zephlebia dentata* and *Deleatidium* sp.) with 73 to 87% and 83 to 89% of the individuals at the native and pine sites, respectively, being mayflies. Pasture sites had a more even spread of individuals across taxonomic groups with case-less Trichopterans, Dipterans and Ephemeropterans making up 10 to 42%, 23 to 35% and 7 to 22% of the individuals respectively. No significant differences were found between land-uses with respect to taxonomic richness and abundance of individuals in the drift communities ( $F_{2,15} = 1.65$ ,  $P = 0.22$ ;  $F_{2,15} = 0.10$ ,  $P = 0.90$ ).



**Figure 7:** Higher order taxonomic composition of (a) 24 hour drift samples collected in January-March, 1996, in three streams in each of three land-use types: hill country pasture, *Pinus radiata* plantation forest and native broadleaf / podocarp forest and (b) invertebrate assemblages on tiles collected on completion of 42 day colonisation and 24 hour drift samples in each of the land-uses.

Over the three land-use categories the abundance of individuals in each of the taxonomic groups on the colonised tiles was very similar to the composition of the drift (Fig. 7b). In particular the dominance of mayflies in the drift in the forest streams is mirrored in their dominance in the tile communities. Similarly the more even distribution of taxa in the drift at the pasture sites is reflected by a more equitable distribution realised at the end of the colonisation period in the pasture tile communities.

**Table 3.** F statistics for lack of fit tests performed on power and negative exponential curves fitted to taxonomic richness, total abundance, Margalef's index and the Berger-Parker index for collections of invertebrates taken from tiles at the 9 study sites between January 25 and March 9, 1996. Significance at 5% are indicated by \*. Lower F values (i.e., better fit) are indicated by bold print. A sharp sign indicates a complete lack of fit to the model.

Variable	Taxa number		Abundance		Margalef's index		Berger-Parker	
	Power	Negative exponential	Power	Negative exponential	Power	Negative exponential	Power	Negative exponential
<b>Pasture</b>								
PW2	4.505*	<b>1.822</b>	<b>0.222</b>	0.401	3.069*	<b>0.324</b>	#	#
PW3	<b>1.675</b>	#	0.952	<b>0.424</b>	0.923	<b>0.297</b>	<b>0.015</b>	#
PW5	<b>0.553</b>	2.292	<b>1.269</b>	2.398	<b>0.141</b>	1.432	#	#
<b>Pine</b>								
EM1	<b>1.056</b>	2.036	1.578	<b>1.309</b>	<b>1.233</b>	3.127*	#	#
EM2	<b>0.380</b>	1.672	0.213	<b>0.142</b>	<b>0.623</b>	2.072	#	#
ES	<b>0.588</b>	1.761	0.204	<b>0.185</b>	<b>0.267</b>	2.203	#	#
<b>Native</b>								
NF	0.658	<b>0.017</b>	1.480	<b>0.855</b>	<b>0.139</b>	0.654	#	#
NKL	2.969*	4.083*	1.681	<b>1.019</b>	<b>2.100</b>	3.025*	#	#
NW5	<b>1.618</b>	4.828*	<b>2.829</b>	3.911*	<b>0.989</b>	5.942*	#	#

## DISCUSSION

Both taxonomic richness and abundance of individuals were found to be greater at the pasture sites compared to forest sites. Diversity (Margalef's index) was also higher at the pasture sites at least during the early stages of colonisation.

Conversely, dominance (Berger-Parker index) was most pronounced at the pine forest sites where *Deleatidium* sp., *Zephlebia dentata* and *Coloburiscus humeralis* usually accounted for the bulk of the individuals.

Changes in land-use from native podocarp / broadleaf forest to pasture and subsequent conversion to exotic pine forest had a number of effects on the colonisation dynamics of aquatic invertebrates in these streams. Time taken for colonisation was assessed in two ways; (1) when community characteristics measured (taxonomic richness, abundance, etc.) reached a plateau and (2) when the community characteristics showed no significant difference to those measured for the substrate. Taxonomic richness and diversity (Margalef's index), peaked in the pasture and pine forest streams within the 42 day colonisation period, while colonisation in the native forest streams was much slower. However, with the exception of three sites, colonisation in terms of abundance was, not achieved in 42 days (i.e., abundance was still increasing). Dominance, as expected, decreased with time as colonisation proceeded at most study sites. When communities colonising the tiles were compared with those of the substrate pasture sites were colonised most quickly, followed by pine, while native sites exhibited no clear pattern. In contrast to above, at most sites abundance reached comparable levels to that of the undisturbed substrate far more quickly than did taxonomic richness.

A negative exponential function is indicative of colonisation nearing "completion", in contrast to the more continuous process indicated by a power function. The colonisation models indicated colonisation, in terms of abundance, proceeded more

quickly than for taxonomic richness or diversity. However, the models gave no clear indication that land-use affects the colonisation pattern, as modelled by these functions anyway.

As taxonomic richness and abundance of individuals in drift showed no significant differences between land-uses it would seem unlikely that drift could account for differences in colonisation rates. While some studies have found drift abundance to be greater in areas of high benthic abundance (Mathoko and Mavuti, 1992), drift was not greater in the more densely populated pasture sites. However the composition of the drift did differ with land-use and these differences were mirrored by differences in the composition of the resultant tile communities. This suggests that while drift did not effect the rapidity of colonisation it did have an effect on the composition of the colonising fauna. The importance of drift in the colonisation of new substrates is well documented e.g., Williams and Hynes (1976), Townsend and Hildrew (1976) and Gore (1979) and it is obvious that land-use affects the particular taxa available to drift in the substrate.

The disturbance and removal of riparian vegetation allowing greater solar radiation and increases in water temperature is likely to have been the cause of the greater periphyton levels at the pasture sites (Hill and Harvey, 1990; Boston and Hill, 1991). In turn this periphyton abundance seems likely to have accounted for the increased abundance of individuals and/or taxonomic richness at these sites (Robinson and Minshall, 1986; Death and Winterbourn, 1995). Increases in abundance may also have contributed to increases in taxonomic richness through passive sampling effects (Huston, 1994). Roby *et. al.* (1978), Meier *et. al.* (1979) and Mathooko (1995) considered the build-up of periphyton and organic detritus to be the most important factor governing colonisation. The similarity between the communities of the two forest land-use types (Fig. 7b) suggests the lower water quality and increased sedimentation present at the modified sites did not play a major role in producing the differences in colonisation found between land-uses (Quinn *et. al.*, 1994).

Overall, pasture followed by pine streams recovered more quickly than their native counterparts. Rapid recovery, according to Reice (1985), is evidence of a resilient community structure, so presumably, the communities of the modified streams are better able to colonise new substrates than those of the non-impacted streams. Prior land-use disturbance of the pasture and pine catchments may work to eliminate less resilient species leaving only good colonisers in these communities. Mackay (1992) suggests food resources, hydrologic regime and dominant taxa are the most important factors in determining the overall resilience of a stream community. As stated above differences in food resources were certainly a factor in this study. Although current velocities were higher in pasture streams Quinn *et al.* (1994), Quinn suggests this was unlikely to have been responsible for differences in the communities of these streams based on species' water velocity preferences. Unfortunately no other hydrologic variables were measured. Taxonomic differences in dominant colonists between land-uses were apparent and were likely to have been an additional factor affecting colonisation.

Unfortunately it is difficult to assess the effects of land-use induced disturbance on colonisation in other studies as land-use is often not described in detail where factors such as drift (Townsend and Hildrew, 1976; Williams and Hynes, 1976) or hydrologic disturbance (Malmqvist and Otto, 1987) are the primary focus. Studies are also often confined to single land-use types. However, in studies situated in land-use types as diverse as braided rivers (Sagar, 1983), pasture (Williams and Hynes, 1977; Meier *et al.*, 1979), high altitude mixed indigenous - exotic woodland (Mathooko and Mavuti, 1992; Mathooko, 1995), reclaimed strip-mined land (Gore, 1979) and oak / bay and coniferous forests (Roby *et al.*, 1978) colonisation times between 10 and 90 days are normal, although there is some evidence of longer colonisation times (Williams and Hynes, 1977). It is evident, from the studies above and this one, that colonisation is generally rapid across a wide range of land-use types.

In summary, land-use does influence colonisation although interpretation is dependant on how colonisation is assessed (i.e., graphical, colonisation models or comparisons of colonist and surrounding substrate communities). The more

abundant and quickly accruing periphyton, providing greater food resources and habitat complexity in the pasture streams may account for the more rapid colonisation in these streams. Alternatively, land-use induced disturbance in the pasture and pine catchments eliminating less resilient taxa and leaving the most able colonisers may explain why colonisation proceeds more rapidly in these streams.

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## **CHAPTER 3:**

# **THE EFFECT OF LAND-USE ON BENTHIC INVERTEBRATE COMMUNITY STRUCTURE AND RESILIENCE.**

## THE EFFECT OF LAND-USE ON BENTHIC INVERTEBRATE COMMUNITY STRUCTURE AND RESILIENCE.

### ABSTRACT

Structure and resilience of invertebrate communities inhabiting 4 streams in each of 3 different land-use categories; hill country pasture, *Pinus radiata* plantation forest and native podocarp / broadleaf forest, were examined during March-April, 1996. Community structure was assessed using detrended correspondence analysis to ordinate sites according to community composition. Community matrices were constructed and eigenvalues extracted to provide an estimate of community resilience. Although community composition was effected by land-use there was no corresponding effect on community resilience and nearly all the communities fell outside the limits for local stability. Resilience appears to depend not on what particular taxa make up a community but on some threshold number being present to allow for normal community function.

**Keywords;** Land-use; disturbance; macroinvertebrates; community structure; community function; community resilience.

### INTRODUCTION

Anthropogenic disturbance resulting from land-use activities such as exotic forestry and pastoral farming has a profound impact on the physical characteristics of streams (Fahey and Rowe, 1992; Prat and Ward, 1994). Changes to catchment land-use have, as a result of this, also brought changes to the structure of the benthic invertebrate communities of the streams that drain these catchments. Changes to structural elements, such as taxonomic richness, abundance, diversity

and composition, of invertebrate communities in response to land development has been well documented in both New Zealand (e.g., Allen, 1959; Winterbourn, 1986; Quinn and Hickey, 1990b; Smith *et al.*, 1993; Townsend *et al.*, 1997) and elsewhere in the world (Dance and Hynes, 1980; Reed *et al.*, 1994; Richards and Host, 1994). Changes in biotic structure are normally considered to be the result of changes to riparian vegetation giving rise to increased light levels and alterations to temperature and discharge patterns, and fertiliser and sediment runoff causing increases to instream nutrient levels and sedimentation (Cowie, 1985; Winterbourn, 1986; Prat and Ward, 1994; Quinn *et al.*, 1994).

From these and other studies it seems clear that changes to land-use can have a dramatic effect on benthic community structure. However, while it is clear that structure is affected it is less clear how, or if, community function is affected. Although the definition of community function is unclear it includes community processes and attributes such as nutrient cycling, food processing and community resilience. The nature of the relationship between community structure (taxonomic richness, diversity, composition, etc.) and function (e.g., nutrient cycling, food processing and resilience) is a current area of much debate amongst the framework of such ideas as ecosystem redundancy (Ehrlich and Ehrlich, 1981; Walker, 1992; Lawton and Brown, 1993; Martinez, 1995). Redundancy in biological systems may be identified if ecosystem function (e.g., biomass, total production, nutrient cycling, resilience, etc.) remains constant while community composition changes (Gitay *et al.*, 1996).

Theoretical studies suggest resilience (one aspect of function) will be related to structure i.e., complexity (number of taxa, connectance and average interaction strength). The traditional view put forward by MacArthur (1955) and Elton (1958) was that complex communities are more stable. This view has since been challenged by mathematical models which suggest less complex communities are more stable (Gardener and Ashby, 1970; May, 1972, 1973).

The aim of this study was to first establish whether community structure is effected by land-use as predicted from the literature. If this is the case I will examine how this change in structure affects one aspect of community function, namely resilience. Resilience is a measure of how quickly communities can recover to their former state following a disturbance (Begon *et. al.*, 1990). That is, are land-use impacted streams less able to cope with further disturbance i.e. floods because their structure (and thus function) has been affected by land-use practices. Specifically, composition and local stability (measured with eigenvalues) of invertebrate communities from 12 streams, 4 in each of 3 different land-use types; hill country pasture, exotic *Pinus radiata* forestry and native podocarp / broadleaf forest, were examined and the relationship between the two aspects of community structure and function evaluated.

## STUDY SITES

The 12 streams in this study are located in 3 land-use categories; hill country pasture (PW2, PW3, PW5 and PP), *Pinus radiata* plantation forest (EM1, EM2, ES and EZ) and native broadleaf / podocarp forest (NF, NKL, NW5 and NN), situated along 13 km of the Hakarimata Ranges, west of Hamilton, New Zealand (175° 15'E; 37° 47'S). The streams are small (third order or less), with the largest less than 3.5 m wide. The catchments of the study reaches are also correspondingly small, with most smaller than 3 km<sup>2</sup> (Smith *et. al.*, 1993) and with the exception of site ES, all are composed entirely of a single land-use category. ES is estimated to be 79% *Pinus radiata* and 21% native broadleaf / podocarp forest (Quinn *et. al.*, 1994). The catchments above the study reaches are dominated by steep (>30°) to hilly topography (Smith *et. al.*, 1993) and site elevation ranges from 35 m to 120 m above sea level (Quinn *et. al.*, 1994).

The pasture streams drain catchments cleared of native forest cover for approximately 60 yrs (Quinn *et. al.*, 1994) and are currently managed for sheep and beef farming. These streams typically have narrow, deep channels and although

**Table 1.** Physico-chemical characteristics of the 12 study reaches. The upper part of the table contains data taken from surveys conducted November 1992 - March 1993 (Smith *et. al.*, 1993; Quinn *et. al.*, 1994), while the lower portion (in italics) contains recordings taken between 26 January and 9 March 1996. N.D. denotes no data was available. \*Catchment is estimated to be 79% *Pinus radiata* forest and 21% native broadleaf / podocarp forest (Quinn *et. al.*, 1994). #The thermometers from these sites were lost during the survey period.

Site code	PW2	PW3	PW5	PP	EM1	EM2	ES	EZ	NF	NKL	NW5	NN
Land-use	pasture	pasture	pasture	pasture	pine	pine	pine*	pine	native	native	native	native
Site elev. (m)	90	100	60	N.D.	50	35	55	N.D.	40	120	70	N.D.
Catchment area (km <sup>2</sup> )	0.95	0.49	2.59	N.D.	0.88	1.31	0.69	N.D.	2.01	0.525	3.00	N.D.
Mean temp. (C <sup>o</sup> )	13.2	16.3	14.2	N.D.	13.5	13.6	12.5	N.D.	12.5	12.2	12.2	N.D.
Max. temp. (C <sup>o</sup> )	15.8	22.7	17.4	N.D.	15.4	15.7	14.7	N.D.	15.2	13.6	14.6	N.D.
Min. temp. (C <sup>o</sup> )	11.0	12.7	11.3	N.D.	12.0	12.0	10.0	N.D.	10.0	10.3	10.1	N.D.
Mean flow (L/s)	16	7	45	N.D.	11	17	8	12	32	10	55	N.D.
pH	7.50	7.40	7.48	N.D.	7.06	7.20	7.53	N.D.	7.62	7.38	7.56	N.D.
E.C.(us/cm)	108.5	88.3	107.1	N.D.	90.4	100.0	96.4	N.D.	122.9	116.4	122.2	N.D.
Turbidity (FTU)	6.0	7.6	5.3	N.D.	21.3	23.5	12.0	N.D.	4.1	6.7	4.4	N.D.
<i>Mean temp. (C<sup>o</sup>)</i>	19.2	19.5 <sup>#</sup>	18.6	N.D.	16.1	16.0	15.0	N.D.	15.1 <sup>#</sup>	14.0	14.9	N.D.
<i>Max. temp. (C<sup>o</sup>)</i>	27.0	26.0 <sup>#</sup>	24.0	N.D.	19.0	18.5	17.5	N.D.	17.0 <sup>#</sup>	17.0	18.0	N.D.
<i>Min. temp. (C<sup>o</sup>)</i>	14.0	14.5 <sup>#</sup>	15.0	N.D.	13.0	14.0	11.0	N.D.	14.0 <sup>#</sup>	12.0	12.0	N.D.
<i>Mean vel. (m/s)</i>	0.131	0.101	0.282	N.D.	0.128	0.113	0.120	N.D.	0.201	0.085	0.138	N.D.
<i>Stream depth (m)</i>	0.070	0.049	0.062	0.068	0.044	0.063	0.056	0.066	0.050	0.051	0.048	0.043
<i>Stream width (m)</i>	1.09	1.05	1.26	1.10	0.93	1.14	1.96	1.04	1.24	1.41	3.32	1.78

accessible to stock appear relatively stable. Substrate consists of a mixture of silt and gravel with many larger cobbles. Periphyton and macrophyte growth is prolific during late summer at these sites. Also converted to pasture 60 yrs ago, the pine forest catchments were reforested with *Pinus radiata* 17 yrs ago as part of the Ngaruawahia State Forest (Quinn *et. al.*, 1994). These streams are physically unstable with considerable scouring and slumping of the banks, and turbid water. Few large stones are present in these streams with the substrate dominated by fine gravel, silt and woody detritus. Site ES, however, was an exception having a substrate more typical of the native streams in the study (i.e., more stable and less dominated by fine particles). The native broadleaf / podocarp forest is drained by streams of a wider and shallower profile than those in the other land-use areas. Although having predominately gravel substrates, large stones and patches of bedrock are common in these streams. Site characteristics are recorded in Table 1.

## METHODS

### Invertebrate sampling

Invertebrates were collected from stones during March and April 1996 in riffles at 12 sites, 4 streams in each of 3 land-use categories; hill country pasture (PW2, PW3, PW5, PP), *Pinus radiata* plantation forest (EM1, EM2, ES, EZ) and native podocarp / broadleaf forest (NF, NKL, NW5, NN). Fifteen stones, from 3 size divisions (maximum linear, planar dimension <60 mm, 61-90 mm and 91-180 mm) were sampled at each site. Moving progressively upstream, a 250  $\mu$ m mesh dip net was placed behind each stone into which the stone was quickly lifted. Invertebrates were removed with a scrubbing brush and preserved in 70% isopropyl alcohol. Care was taken not to disturb neighbouring stones, but any invertebrates directly below the stone were collected by agitating the substrate to a depth of 10 mm.

Macroinvertebrates were identified and enumerated to the lowest possible taxonomic group using available keys. Taxa not able to be identified were assigned to apparent morphospecies.

Physico-chemical characteristics of the 12 sites including temperature, water velocity and channel dimensions, were measured as part of a related study (Chapter 2). Additional environmental data was taken from surveys conducted on the streams from November 1992 to March 1993 (Smith *et al.*, 1993; Quinn *et al.*, 1994).

### **Community structure analysis**

Similarities in the overall composition of the invertebrate communities collected at the 12 sites was assessed using detrended correspondence analysis (DECORANA) with the statistical package PC-ORD (McCune and Mefford, 1995). PC-ORD was also used to correlate environmental measures and taxonomic data to the ordination. The SYSTAT (1996) statistical package was used to perform analysis of variance (ANOVA) on measures of structure and function for the communities of the 3 land-use types.

### **Community resilience analysis**

Community matrices detailing each species impact on each of the other species were compiled following Bruns and Minshall (1983). Matrices were constructed on the basis of possible competitive and predatory interactions evaluated by estimates of resource overlap (e.g., Lawlor, 1980; Bruns and Minshall, 1983; Death, 1996). Evaluating competitive interactions on the basis of resource overlap, while not the most desirable method, was used as the first step in exploring resilience because experimental determination of competitive interactions in such large communities would be difficult. Furthermore, evaluating secondary impacts of a species (e.g., species A competes with species B keeping B's population so low that it exerts a lower predation pressure on its prey than it otherwise would) is difficult

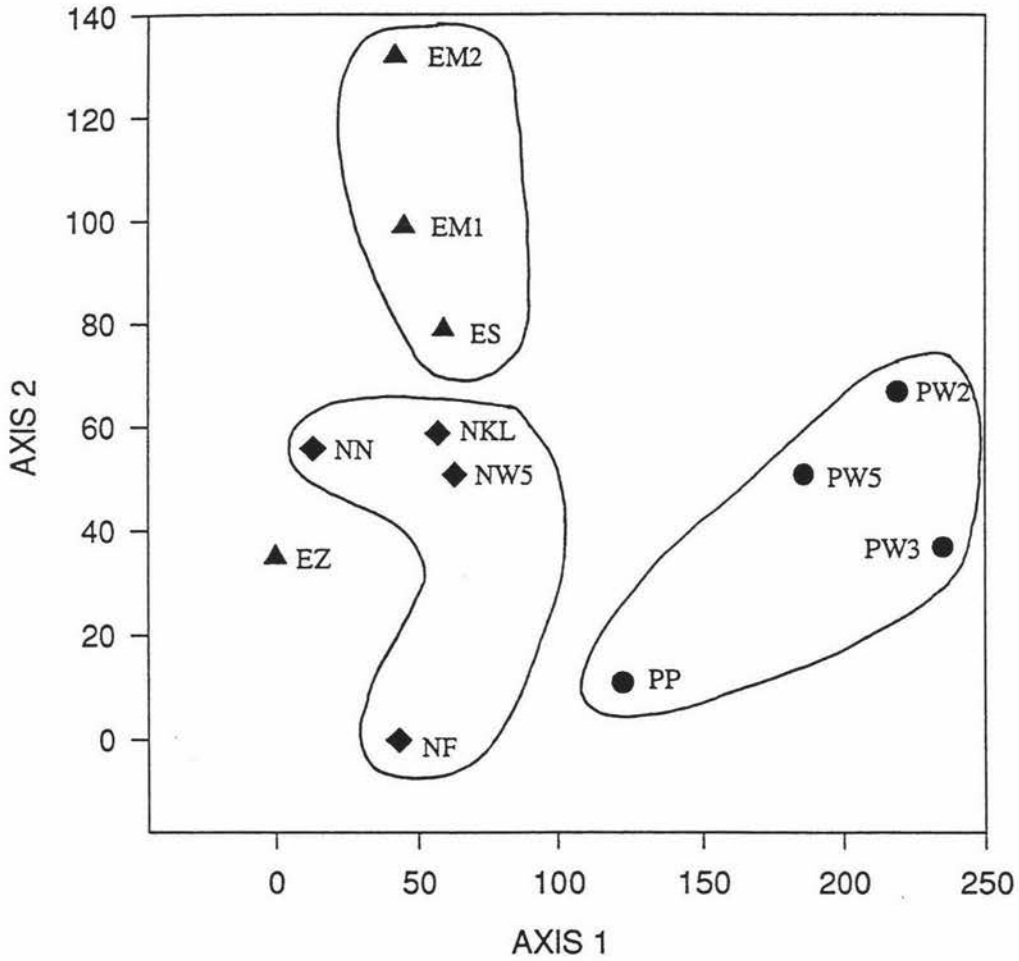
experimentally. Resource (in this case a single stone) overlap, therefore, provides a workable approximation for the calculation of matrix components necessary to examine community stability (Lawlor, 1980; Bruns and Minshall, 1983; Pimm, 1985).

Resource overlap was assessed by pairwise Spearman rank correlations of each species in the community with all other species across the 15 stone samples collected at each of the 12 sites. Species which occurred as single individuals were eliminated from the analysis together with any double-zero matches (Legendre and Legendre, 1983). Interaction coefficients were set at zero for non-significant correlations, whereas negative correlations (excluding predator and prey) were determined to indicate competitive interactions. Positive correlations (excluding predator and prey) were taken to signify weak or nil interactions and were given an interaction term of zero. Although competition may result in either positive or negative associations evidence suggests negative associations are the more likely result in streams (e.g., McAuliffe, 1984a, 1984b; Hart, 1985; Hawkins and Furnish, 1987; Hemphill, 1988; Dudley *et al.*, 1990). Intraspecific interactions were assigned a value of -1 following Pimm (1982). Significant correlations between predators and prey were considered to be the result of predation rather than competition for resources, and were assigned positive terms for predators and negative for prey. Matrix eigenvalues were extracted using PC-Matlab (Moler *et al.*, 1987).

## RESULTS

### Community structure

Abundance of individuals collected at the 12 sites varied from 2267 at pasture site PP to 345 at native forest site NKL (Table 2). PP also had the greatest taxonomic richness of 43 while pine forest site EM1 had the least with 20. Pasture sites were numerically dominated by *Potamopyrgus antipodarum*, Elmidae larvae and



**Figure 1.** Detrended correspondence analysis of invertebrate communities collected from 15 stones in 12 streams in three land-use types between March and April 1996. Hill country pasture (circles), exotic pine forest (triangles) and native podocarp / broadleaf forest (diamonds).

**Table 2.** Community structure and function characteristics for invertebrate communities of 12 streams in the Whatawhata-Ngaruawahia area of Waikato, collected in March-April 1996. Sites PW2 through PP represent sites on hill country pasture streams, EM1 to EZ represent exotic pine forest sites and NF to NN represent native podocarp / broadleaf forest sites.

Site	PW2	PW3	PW5	PP	EM1	EM2	ES	EZ	NF	NKL	NW5	NN
Max. eigenvalue	1.03	0.58	0.47	0.76	0.34	0.38	1.05	-0.05	0.28	-0.16	0.23	0.316
Min. eigenvalue	-1.13	-3.07	-2.77	-3.57	-2.34	-2.38	-4.04	-1.93	-3.45	-1.84	-2.21	-3.11
Max. negative eigenvalue	-0.19	-0.12	-0.25	-0.06	-0.41	-0.36	-0.05	-0.05	-0.12	-0.16	-0.44	-0.01
Dom. eigenvalue	-0.99	-0.94	-0.99	-0.94	-0.48	-0.90	-0.96	-0.99	-0.98	-0.94	-0.89	-0.82
Abundance	441	1533	764	2267	458	706	741	449	484	345	565	661
Taxonomic richness	24	28	27	43	20	26	31	25	30	26	28	23
Connectance	0.06	0.09	0.08	0.10	0.07	0.03	0.08	0.11	0.07	0.09	0.11	0.08
Interaction strength	0.81	0.74	0.73	0.80	0.73	0.76	0.78	0.88	0.79	0.80	0.84	0.77
Positive interact'ns	16	17	12	68	9	11	17	28	15	27	25	10
Negative interact'ns	15	49	45	120	19	19	55	38	45	32	46	30
Dominant taxa	<i>Potamo-pyrgus</i>	<i>Potamo-pyrgus</i>	Elmidae Larvae	<i>Deleati-dium</i>	<i>Z dentata</i>	<i>Z dentata</i>	Hydropsychidae	<i>Coloburiscus</i>	<i>Deleati-dium</i>	Hydropsychidae	<i>Deleati-dium</i>	<i>Coloburiscus</i>
Margalef's index	3.78	3.68	3.92	5.44	3.10	3.81	4.54	3.93	4.69	4.28	4.26	3.39
Berger-Parker index	0.29	0.40	0.19	0.43	0.31	0.36	0.24	0.23	0.20	0.25	0.42	0.36

*Deleatidium* sp. while at forest sites *Zephlebia dentata*, early instar Hydropsychidae, *Deleatidium* sp., and *Coloburiscus* sp. were most abundant. Detrended correspondence analysis of the invertebrate communities shows a clear separation according to land-use with the exception of EZ (Fig. 1). Axis 1 separates the pasture sites from the forest sites, while pine forest sites EM1, EM2 and ES are separated from the other forest sites on axis 2. Positive correlations

**Table 3.** R-values for significant Pearson and Kendall correlations between particular taxa and the axes of a detrended correspondence analysis (Fig. 1) of invertebrate communities collected from 4 streams in each of the 3 land-use types in March-April, 1996.

Correlations with axis 1.	R	Correlations with axis 2.	R
Positive correlations			
<i>Aoteapsyche</i> sp.	0.894	<i>Icthybotus</i> sp.	0.581
<i>Austroclima</i> sp.	0.808	<i>Zephlebia dentata</i>	0.713
Elmidae larvae	0.565	Amphipoda sp.	0.652
<i>Hydrobiosis parumbripennis</i>	0.610		
<i>Oxyethira albiceps</i>	0.809		
<i>Physa</i> sp.	0.641		
Oligochaete sp.	0.706		
<i>Potamopyrgus antipodarum</i>	0.688		
<i>Lymnaea columella</i>	0.753		
Chironomid sp. A	0.577		
Negative correlations			
<i>Acanthophlebia cruentata</i>	-0.670	<i>Stenoperla prasina</i>	-0.671
<i>Coloburiscus</i> sp.	-0.568	<i>Orchymontia</i> sp.	-0.553
<i>Orthopsyche thomasi</i>	-0.602	<i>Zelandobius furcillatus</i>	-0.641
<i>Podaena</i> sp.	-0.557		

with axis 1 were found for taxa associated with pasture sites and negative correlations for taxa associated with forest sites (Table 3). Positive correlations with axis 2 were also found for taxa associated with pine forest sites and negative correlations for those associated with native forest sites. Surprisingly, there was no significant difference between communities of different land-use types in terms of abundance or diversity as assessed as taxonomic richness, Margalef's index (Clifford and Stephenson, 1975) and the Berger-Parker index (Berger and Parker, 1970) (Table 4). No significant correlation between any environmental measure

taken at the sites (temperature, conductivity, pH, flow, velocity, catchment area, site elevation, stream depth, stream width and periphyton total pigment) and the DECORANA axes was found.

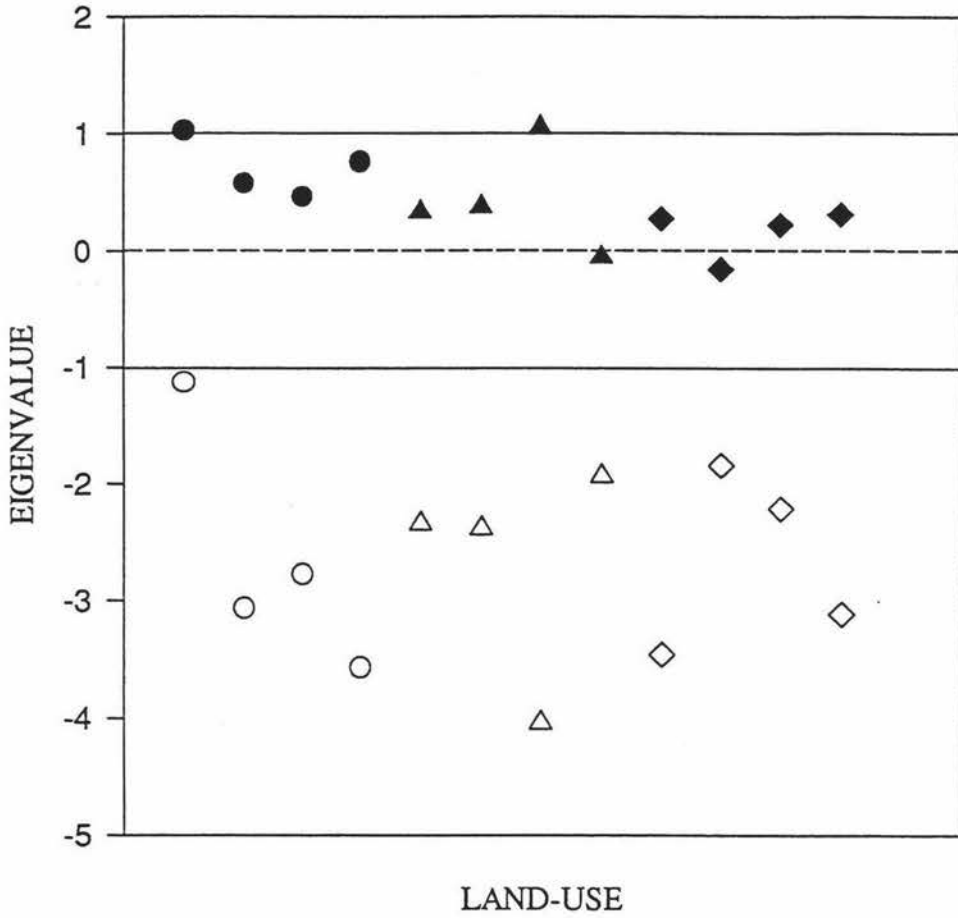
**Table 4.** F-values, degrees of freedom and P-values for ANOVAs performed on measures of community structure and function for communities of 12 streams collected in March-April, 1996, in three land-use types in the Whatawhata-Ngaruawahia area of Waikato.

Variables	F-value	d.f.	P-value
Land-use			
v. abundance	2.78	2,9	0.12
v. taxonomic richness	0.80	2,9	0.48
v. margalef's index	0.34	2,9	0.72
v. berger-parker index	0.21	2,9	0.81
v. maximum negative eigenvalue	0.16	2,9	0.85
v. dominant eigenvalue	0.85	2,9	0.46
v. connectance	0.42	2,9	0.67
v. average interaction strength	0.40	2,9	0.68
Taxonomic richness			
v. connectance	1.29	1,10	0.28
v. average interaction strength	0.27	1,10	0.62
Maximum negative eigenvalue			
v. taxonomic richness	1.43	1,10	0.26
v. connectance	0.65	1,10	0.44
v. average interaction strength	0.53	1,10	0.48
Dominant eigenvalue			
v. taxonomic richness	2.17	1,10	0.17
v. connectance	0.08	1,10	0.78
v. average interaction strength	2.16	1,10	0.17

### Community stability

In all but one site more negative than positive associations between taxa were observed (Table 2). Maximum and minimum eigenvalues extracted from the community matrices of the 12 sites are plotted in Fig. 2.

Stability criteria differ depending on the underlying structure of the matrix, namely whether species population growth is best modelled by

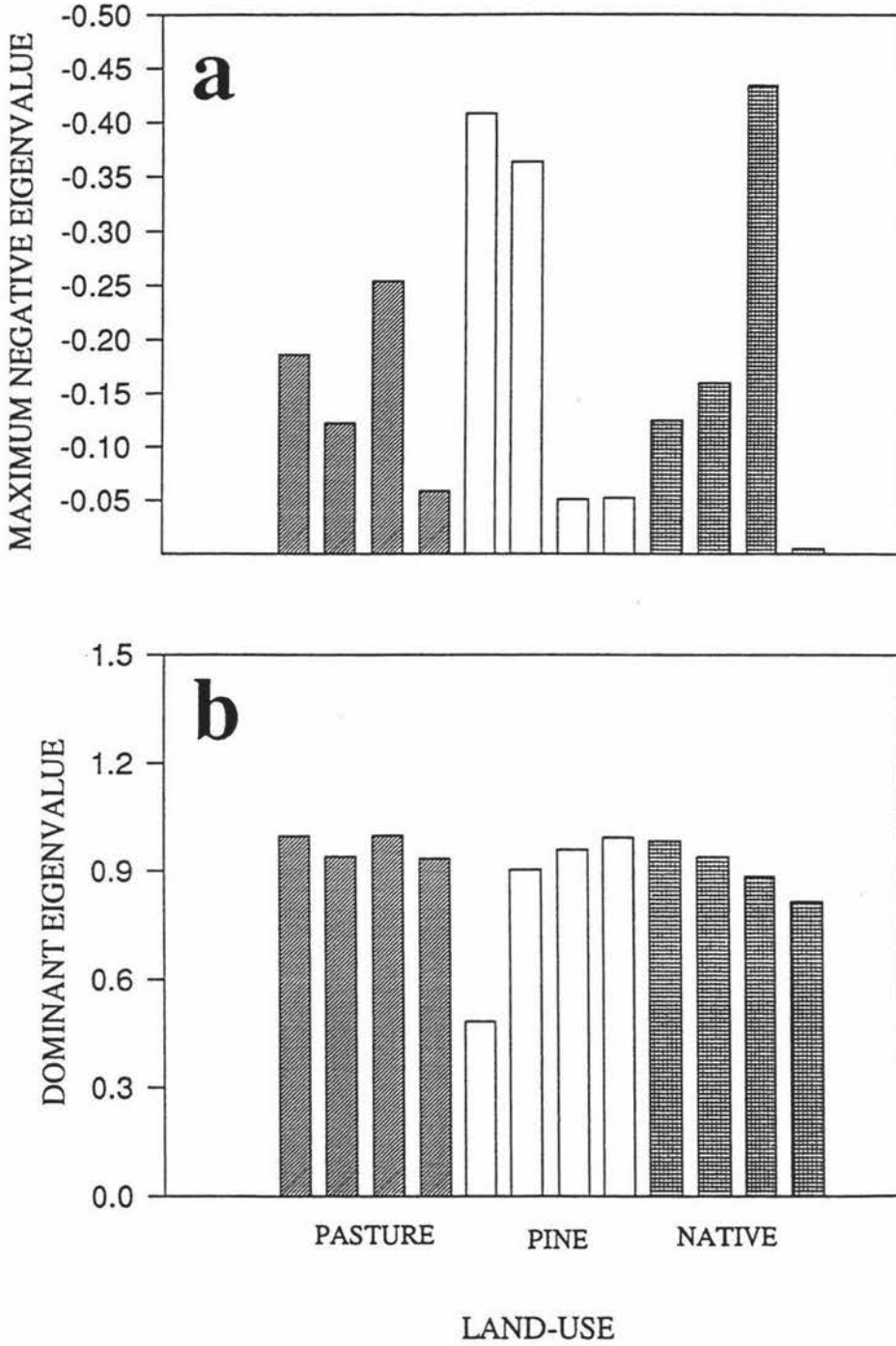


**Figure 2.** Maximum (solid symbols) and minimum eigenvalues (open symbols) for community matrices collected at 12 sites in March and April 1996, as a function of land-use. Hill country pasture (circles), exotic pine forest (triangles) and native podocarp / broadleaf forest (diamonds). The area within the entire lines is the stability criterion for matrices based on difference equations and the area below the broken line is the criterion for stability for a differential equation based system.

differential or difference equations. These populations are likely to be modelled by equations which fall somewhere between the two types (Death, 1996), so stability criteria for both types of equation were considered. To be stable under a differential equation based system all eigenvalues must have negative real parts, while for stability under a difference based system the square of both the real and imaginary parts of the eigenvalues must be less than one (Pimm, 1982).

Eigenvalues of all but two sites are clearly outside the stability criteria for both equation types. Pine forest site EZ and native forest site NKL, the exceptions, have eigenvalues which lie within the stability criterion for a differential based system. Furthermore, although outside the stability envelope for differential systems, native forest streams, followed by pine and pasture streams, had communities closest to this criterion. No sites could be regarded as stable under the difference equation criterion and no pattern in land-use was apparent.

These results suggest that the communities surveyed should not be persistent, however, this is clearly not the case as the communities do not differ fundamentally from those collected at other times at this location (National Institute of Water and Atmospheric Research unpub. data 1992-3) and chapter 2 shows the communities are capable of quickly colonising new substrates. Fig. 3 gives measures of community resilience for the 12 sites (excluding eigenvalues outside the stability envelope). Again criteria are dependent on the type of equation on which the system is based. For differential equation based systems resilience is given by  $-1/(\text{the real part of the largest eigenvalue})$  (Pimm and Lawton, 1977) i.e., the more negative the largest eigenvalue, the quicker the community will return to its pre-disturbance state. The pine forest sites EM1 and EM2 and the native forest site NW5 show the greatest resilience (Fig. 3a). For difference equation based systems the smaller the dominant eigenvalue (the largest eigenvalue ignoring the sign) the more resilient the community. In this case the community at EM1 is most resilient (Fig. 3b), but, overall there was no difference in either resilience character across land-use (Table 4).

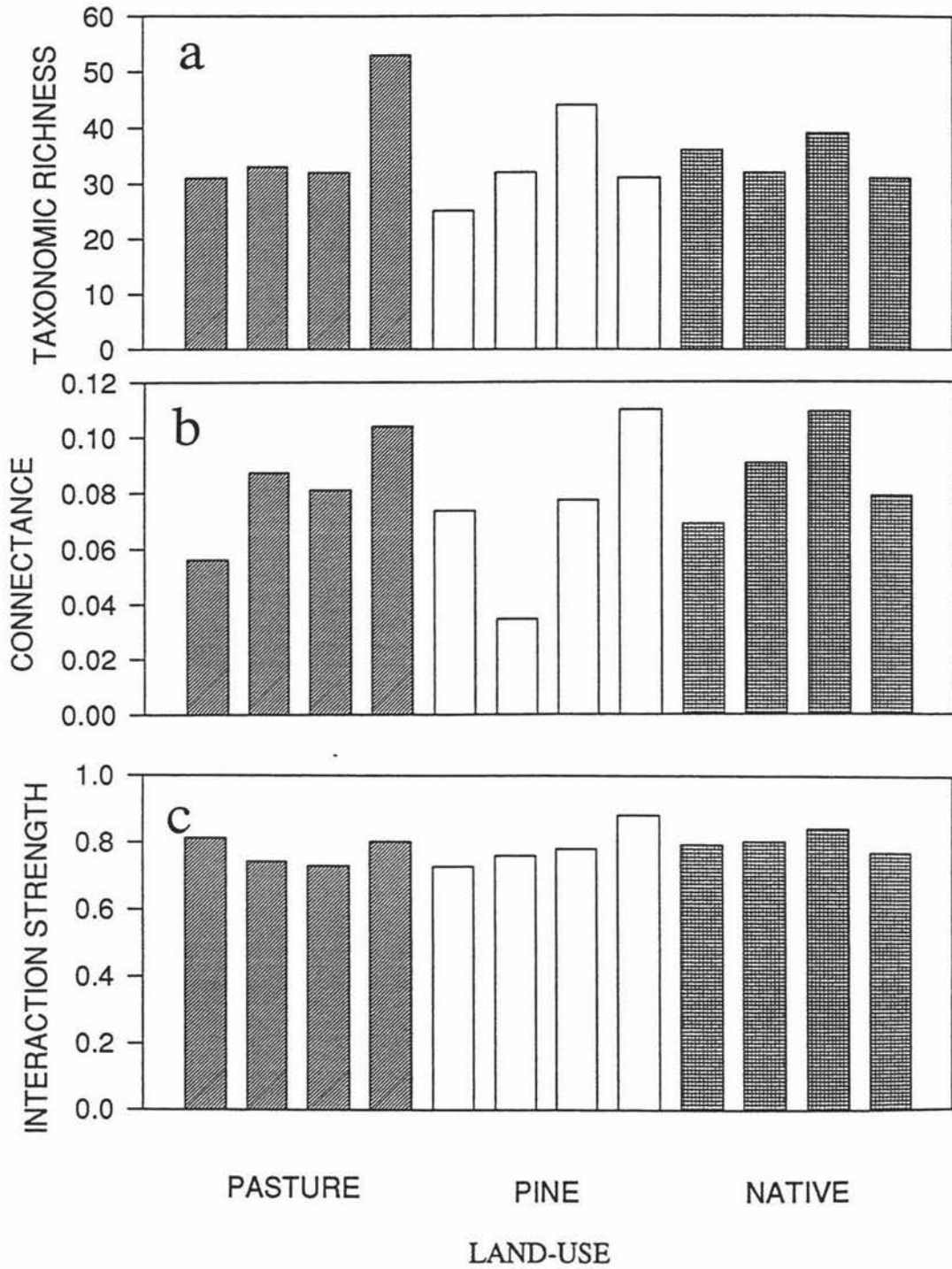


**Figure 3.** (a) Maximum eigenvalue (ignoring all positive eigenvalues) and (b) dominant eigenvalue (ignoring all those equal to or greater than one) as a function of land-use. Hill country pasture (diagonal hatching), exotic pine forest (no hatching) and native podocarp / broadleaf forest (reticulated hatching).

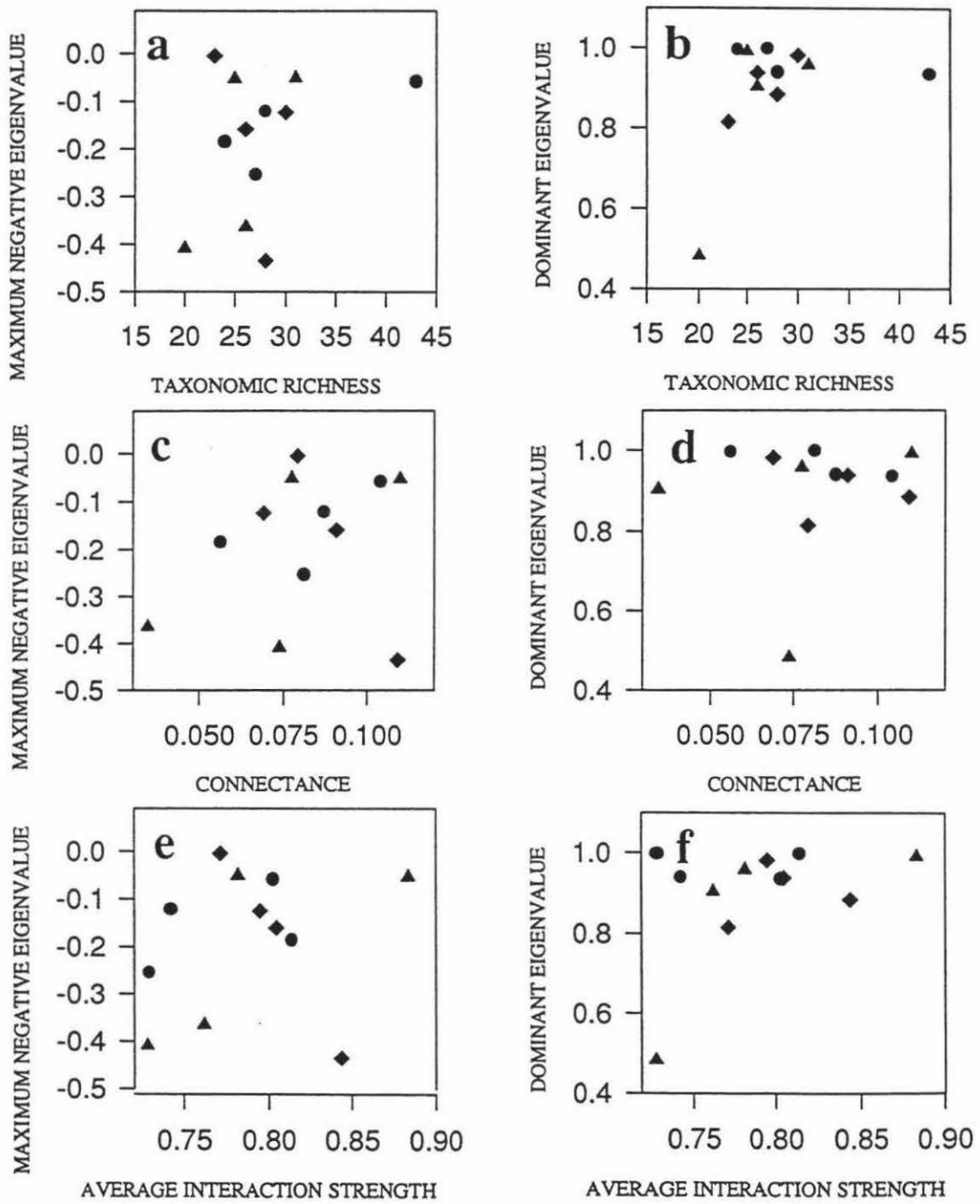
Community complexity as measured by taxonomic richness, connectance and average interaction strength was not significantly different between land-use types (Fig. 4; Tables 2 and 4). If land-use then does not have a major affect on complexity and consequently community stability and resilience what aspects of the communities examined account for differing resilience between sites? Resilience is plotted against a number of measures of community complexity; taxonomic richness, connectance and average interaction strength in Fig. 5. No significant interactions were found between resilience and taxonomic richness, connectance or average interaction strength (Table 4). There was also no significant relationship between either connectance or average interaction strength and taxonomic richness (Fig. 6; Table 4).

## DISCUSSION

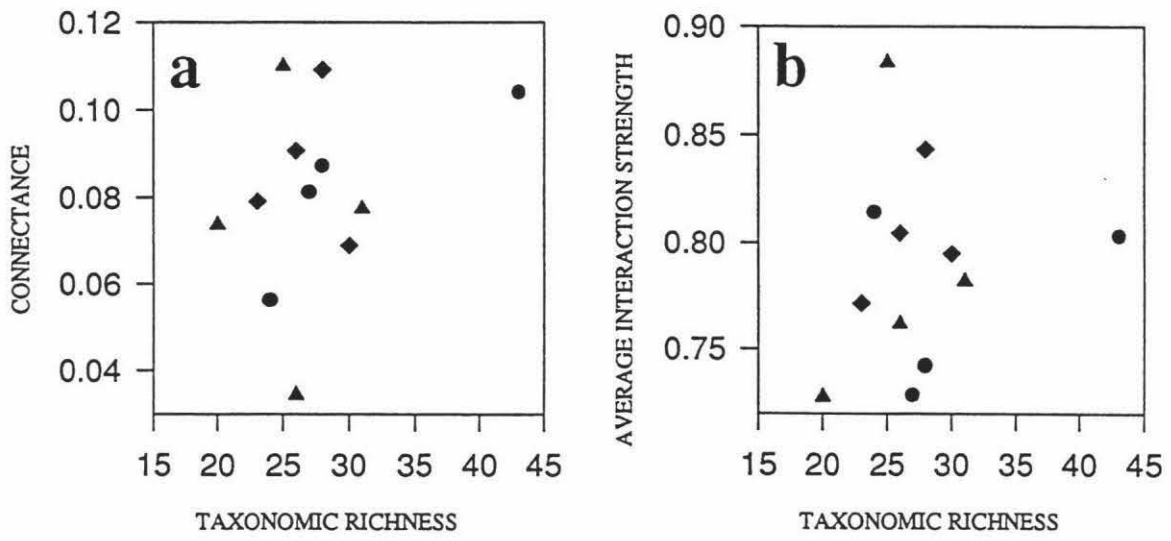
Although land-use changes at Whatawhata have had no significant effect on the abundance and diversity of lotic invertebrate communities they have markedly effected community composition. A detrended correspondence analysis clearly separated pasture sites from forest sites while 3 of the 4 pine sites were shown to be distinct from the rest of the forest sites. The lack of any significant effect of land-use on diversity and abundance is surprising and contrasts with the findings of others. A number of studies have found land-use changes to effect invertebrate abundance (Townsend *et. al.*, 1997), diversity (Dance and Hynes, 1980; Quinn and Hickey, 1990b; Richards and Host, 1994) and taxonomic composition (Quinn and Hickey, 1990a; Richards and Host, 1994; Townsend *et. al.*, 1997). Furthermore, in a related study (chapter 2), it was found that the communities colonising artificial substrates in these streams were taxonomically richer and more abundant in pasture compared to forest streams, although diversity (Margalef's Index) was not significantly different. However, in accordance with my findings, Reed *et. al.* (1994) found no significant difference in total invertebrate biomass between pasture and forest sites on Australian streams.



**Figure 4.** Taxonomic richness (a), connectance (b) and average interaction strength (c) of the communities from 12 streams in three land-use types. Hill country pasture (diagonal hatching), exotic pine forest (no hatching) and native podocarp / broadleaf forest (reticulated hatching).



**Figure 5.** Maximum negative eigenvalue (ignoring all positive eigenvalues) as a function of taxonomic richness (a), connectance (c) and average interaction strength (e) and dominant eigenvalue (ignoring all those equal to or greater than one) as a function of taxonomic richness (b), connectance (d) and average interaction strength (e). Four streams from each land-use are represented; circles denote pasture streams, triangles pine forest streams and diamonds native forest streams.



**Figure 6.** Connectance (a) and average interaction strength (b) as a function of taxonomic richness. Four streams from each land-use are represented; circles denote pasture streams, triangles pine forest streams and diamonds native forest streams.

Previous studies suggest elevated light and temperature levels resulting from the removal of riparian vegetation and increased nutrient levels from fertiliser and soil runoff are expected to lead to greater algal growth and in turn increased abundance of invertebrates at pasture sites (Quinn *et. al.*, 1992, 1994; Quinn and Hickey, 1990b; also see Minshall, 1984). It is also expected that diversity would decline at the pasture sites because of elevated temperatures and reduced oxygen leading to the loss of intolerant taxa such as Plecoptera (Quinn and Hickey, 1990b; Quinn *et. al.*, 1994). Increased sedimentation would also be expected to decrease diversity in the modified sites (Quinn and Hickey 1990b; Ryan, 1991; Richards and Host, 1994). The fact that diversity and abundance were not affected in my study while composition was suggests the removal of riparian vegetation at Whatawhata has lead to changes in community composition while factors responsible for changes in diversity and abundance in other studies, particularly water quality and substrate characteristics, did not differ strongly enough between land-uses to have a influence on diversity and abundance.

Despite the demonstrated affect of land-use on community composition no corresponding affect was found on community function as measured by resilience; although the majority of community matrices were outside the limits for local stability. There is some debate about the validity of this approach to assessing resilience, especially given the finding of largely unstable communities, however, Bruns and Minshall (1983) and Death (1996) have both shown its usefulness in exploring the relationship between community structure and disturbance.

The lack of any relationship between resilience and measures of complexity (i.e., number of taxa, connectance and average interaction strength) is also interesting in that it is counter to the predictions of numerous ecological studies on both sides of the stability - complexity debate. The traditional view in this debate holds that stability is increased by increased complexity (MacArthur, 1955; Elton, 1958), while the opposite view, developed from mathematical models, has shown less complex systems to be more stable (Gardener and Ashby, 1970; May, 1972, 1973).

A number of studies have shown support for this latter view; resilience decreases with an increase in species number (Bruns *et. al.*, 1982; Bruns and Minshall, 1983; Death, 1996).

However, the critical point in my study is that although a selection of streams from differing catchment land-uses were examined the communities at these sites did not differ markedly in complexity. It is therefore not surprising that land-use had no effect on resilience; the communities did not differ enough in complexity to show any trend in resilience associated with a change in species number, etc. What is surprising, however, is that although community structure i.e., composition, was markedly different between land-uses this did not effect community function i.e., resilience. This contrasts with the findings of chapter 2. where communities were found to have differences in structure (abundance and taxonomic richness) and these differences were reflected in differential rates of colonisation between land-uses. It would be expected that pasture sites, showing the most rapid colonisation, would also have the greatest resilience. This, however, was not the case as nearly all the communities were outside the limits for local stability and resilience did not differ significantly between land-uses although native sites, followed by pine and pasture, were the closest to the stability criterion for differential equation based systems. Resilience (at least at this scale) appears to depend not on which particular taxa are present at a given site but on some threshold number of taxa being present to allow for normal community function (nutrient cycling, primary and secondary production, etc.). This suggests that some species could be exchanged without any change to resilience as long as some minimum number are retained. This lends support to some middle ground between the redundancy and rivet hypotheses of species diversity. The redundant species theory maintains species richness to be irrelevant; many species contribute little to community integrity and can be removed without detriment to their community and only a few key species are needed to maintain ecosystem function (Walker, 1992; Lawton and Brown, 1993; Gitay *et. al.*, 1996). Opposed to this theory is the rivet theory of Ehrlich and Ehrlich (1981) which suggests all species play a small but significant role in ecological systems and the removal of any species will be detrimental at

least in a small way and if too many species are removed ecosystem function will suffer. Gitay *et al.* (1996) suggest a number of ways to identify redundancy in ecological systems including examining some overall measure of ecosystem function (e.g., biomass, nutrient cycling, resilience, etc.) which should stay constant, or nearly so, even though species composition may change. This is certainly the case in my study. Walker (1992) suggested that redundancy is likely to be found in communities that are constructed of functional groups or guilds where a number of species perform similar community functions (e.g., filter feeding, shredding, predation, grazing). Given the generalist feeding habitats, broad habitat requirements and flexible, poorly synchronised life histories of New Zealand's stream invertebrates (Winterbourn *et al.*, 1981), some degree of redundancy seems highly likely.

Given the marked differences in land-use and community composition it is surprising there was no change in resilience. This raises the possibility that local stability may not be the appropriate level at which to examine the stability of these communities or that resilience was not the most appropriate measure of community function. Investigation into the effects of land-use induced changes to community structure on other community functions such as functional group composition, resource depression, nutrient cycling and food processing, may be of value.

In summary, land-use, while having no effect on community structure as assessed as diversity and abundance, did have an effect on composition. However, despite the change in composition no effect on resilience was detected suggesting community function depends on some threshold number of taxa but not on which particular taxa are present.

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