

Land-use influences on New Zealand stream communities: effects on species composition, functional organisation, and food-web structure

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Abstract We used standardised techniques to assemble 18 food-webs in streams subject to four land uses; exotic pasture, native tussock, native forest, and pine plantation. There were clear differences in the algal productivity and standing crops of organic matter between the forested (native and pine) and grassland (tussock and pasture), but not within each grouping. Algal productivity was more than twice as high in the grassland sites, whereas the converse was true for organic matter standing crop. These differences in energy resources were correlated with differences in community composition and food-web structure. Although all streams had a generalist core of species, certain species of algae and invertebrates were predictably associated with either forested or grassland sites. Food-web structure in the forested and grassland sites was also distinct. Grassland food-webs were complex, highly internally connected, and typified by a “triangular” shape. Forested food-webs in contrast were less highly connected, tended to have fewer trophic levels, and were “squarer” in shape. These results provide some support for the concept that energy supply may be an important contributing factor influencing stream community structure. In terms of riparian management, the results emphasise the importance of protecting

representative vegetation around streams to protect stream communities.

Keywords land-use; stream; food-web structure; productivity

INTRODUCTION

A growing awareness of the importance of the lateral linkages between streams and their riparian margins has been a characteristic of studies in stream ecology in the last two decades. Land-use effects have been suggested to have profound influences on stream food-webs at both local and landscape spatial scales (Woodward & Hildrew 2002). A variety of studies have shown that riparian land use has a pervasive effect on stream hydrology (e.g., Fahey & Jackson 1997), geomorphology (e.g., Leeks 1992; Davies Colley 1997), water chemistry (e.g., Hildrew & Ormerod 1995; Friberg et al. 1997), and supply of allochthonous materials (e.g., Edwards & Huryn 1995). All of these effects have important consequences for the biological communities that occur within streams. It is therefore not surprising that a wealth of studies have described differences in the taxonomic composition of invertebrate communities in streams with different riparian land uses. Hopkins (1976) observed lower invertebrate production in a forested compared with unshaded stream reach in the Tararua Ranges. More recent studies have shown the influence of riparian land use on invertebrate community structure (e.g., Harding & Winterbourn 1995; Quinn et al. 1997; Townsend et al. 1997a; see Quinn 2000 for a review). Pasture streams have been shown to have higher invertebrate densities, and a number of taxa have been associated with pastoral settings (Quinn 2000).

Although a number of studies have described differences in the taxonomic composition of invertebrate communities in streams with different riparian land uses, few have explored the implications that this has for the functional organisation and community structure of the streams. Differences

in the characteristics of streams under different land-use regimes provide an opportunity to explore fundamental questions in ecology. For instance grassland streams, which are largely open to sunlight and in pastoral systems are often affected by nutrient inputs, are likely to be more productive than forested streams. Several hypotheses have been presented on the likely effects of productivity on community structure. Lindemann (1942) hypothesised that more trophic levels should be present in more productive systems, and Pimm (1982) formalised this as a hypothesis that food chains should be longer in those systems. Huston (1994) suggested that species richness should be highest at intermediate levels of productivity, and lower at extremely high and low levels.

In this study we build on our earlier work describing the connectivity food-webs of benthic communities in 10 streams in pasture grassland and native tussock grassland (Townsend et al. 1998). That study used measurements of species richness (overall and in different functional groups), connectance, mean food chain length, and dietary specialisation to investigate the relationship between resource availability, disturbance, and food-web architecture. Disturbance was found to be an important determinant of species richness and dietary specialisation, but food chain length displayed a positive relationship with primary productivity. The present study describes an additional eight sites in forested land-use types. The same food-web attributes used by Townsend et al. (1998) are included here plus additional measures of food-web shape (predator:prey ratios) and functional organisation. Invertebrate biomass is partitioned into different functional feeding classes in the expectation that biomass may be more likely than abundance or species richness to be correlated with differences in energy availability.

We describe the taxonomic composition and functional organisation of stream food-webs in streams with different riparian land uses and seek causative mechanisms which may explain any differences that we observe.

METHODS

Study sites

The 18 study sites represent four land-use types in the southern part of the South Island of New Zealand. Ten of the sites (pasture and tussock) have been described elsewhere (Townsend et al. 1998). All sites

are 30 m reaches incorporating pools and riffles in second or third order streams with cobble or pebble beds. Sites were chosen to avoid local human impacts (such as forest clearance or vehicle crossings) and to have catchments dominated (>70% cover) by the desired vegetation type. Sampling occurred in summer (November–January) of 1995/96 (pasture, tussock, and native forest sites) and 1997/98 (pine sites). The rainfall in the 3 months preceding sampling was 75.0 mm (1995) and 78.3 mm (1997), somewhat lower than the 10 year average for the area of 82 mm (NIWA 2000), but comparable between sampling occasions. None of the sites had been subjected to a high flow event in the 3 months preceding sampling.

Land-use types

The two native forest sites are in drainages of mixed broadleaf forest dominated by non-deciduous broadleaf species including *Griselinia littoralis* and *Pseudopanax* sp. A variety of understorey species are present, including *Hebe* spp., several fern species, and the deciduous *Fuschia excorticata*. The six pine streams flow through catchments of mature (>30 years old) *Pinus radiata*. The trees are large (>30 m tall) and produce complete canopy closure along the length of the stream. The sites are typified by limited undergrowth, primarily of exotic Himalayan honeysuckle (*Leycesteria formosa*), native shrubs in the *Hebe* genus, and native crown ferns (*Blechnum* spp.). All the sites lack riparian buffering except the Venlaw site which has low pine stem densities close to the stream and has an extensive riparian vegetation of native species such as those described for the native forest streams. The three pasture sites are associated with an extensive sward of exotic grasses dominated by *Agrostis* spp. These sites are intensively grazed down to the stream's edge. The seven native tussock grassland sites occur at higher altitude than the native forest sites. The streams flow through riparian margins of native tall tussock grasses (primarily *Chionochloa rigida*), which are subject to light grazing by cattle and sheep.

Physical characteristics

To describe the physical habitat of each stream, the mean and standard deviation of four physical measures was used. Width, maximum depth, and flow at the swiftest point were measured at 1-m intervals along the reaches (30 measurements for each variable in total). One hundred random substrate particles were collected in each reach and their length along the longest axis measured.

Standard deviations for width, depth, flow, and substrate size were calculated.

Water chemistry

On arrival at a site (1000 h), the water temperature was measured and a 1-litre water sample was taken to determine alkalinity (using a standard titration (American Public Health 1992)), pH (using a standard pH meter), and water chemistry (total nitrogen, nitrate, ammonia, total phosphorus, and dissolved reactive phosphorus using a Chemlab System 4 autoanalyser and standard methods—American Public Health 1992).

Standing crop of organic matter

Organic matter standing crop was measured in the same way as described in Jaarsma et al. (1998) by partitioning organic material from 10 Surber samples (area 0.06 m², mesh size 250 µm) into 250 µm–1 mm (fine particulate organic matter/FPOM) and >1 mm (coarse particulate organic matter/CPOM) fractions. The fine component is likely to have been somewhat underestimated by the size of the sieve used but reflects the mesh size of the Surber sampler. Samples were taken in the thalweg during base flow conditions. Those fractions were weighed, ashed (550°C for 12 h), and reweighed to ascertain the amount of organic matter on the stream bed. Two 500 ml water samples were filtered through pre-weighed Whatman GF-C filters, dried, weighed, then ashed (550°C for 3 h) and reweighed to ascertain availability of organic matter as seston (water-borne organic matter).

Biofilm at each site was measured as ash-free dry weight (AFDW) per m² of substrate using the methods described in Thompson & Townsend (1999). Ten cobbles were gathered at random along the stream reach and scrubbed into individual containers of distilled water. A 15 ml sample from each container was filtered onto pre-weighed Whatman GF-F filters, dried, weighed, ashed (550°C for 3 h), and reweighed to measure the amount of biofilm on each rock. A foil weight/area regression was used to estimate the surface area of each rock.

Algal sampling

Total potential algal production was estimated using a radioactive carbon isotope (7 ml of ¹⁴C-NaHCO₃ (185 MBq ml⁻¹)) within portable chambers (Fuller & Bucher 1991 as modified in Thompson & Townsend 1999). The chambers were placed in shallow (20 cm) pools in bright sunlight (within the study reach for grassland streams, in downstream

clearings for forested sites). Light intensities were high (range 1175–7244 lum/m²) and well above the saturation levels required for photosynthesis (Hill & Boston 1991; Young & Huryn 1996). Thus it can be assumed that light was not limiting in the light chambers and that maximum algal production was being measured for each sample.

Algal species composition was described based on rock scrubblings. Five half-millilitre samples were taken from the rock scrubblings from each site and used to construct wet mounts. These were inspected completely under 200–400× magnification to identify which algal species were present using appropriate texts (see: Thompson & Townsend 2003). Algal taxonomy was checked by photographing species and sending the photographs to local experts to confirm identifications (see Acknowledgments).

Animal sampling

Ten randomly located Surber samples (area 0.06 m², mesh size 250 µm) were taken at each site to sample benthic macroinvertebrates. Fish were sampled using electro-fishing and crayfish by electro-fishing and searching under stones. Ten individuals of each species were selected at random from those collected. These were euthanased and used for gut analysis, the remainder being returned to the stream.

The 10 Surber samples were searched for invertebrates, excluding those less than 1.5 mm, terrestrial invertebrates, partial invertebrates, pupae, and empty insect cases. All macroinvertebrates were measured for length and identified to the highest degree of taxonomic resolution possible using the key of Winterbourn & Gregson (1989). Of the 129 taxa identified at the 18 sites, 45% were identified to species and 79% to genera.

Invertebrate lengths were used to estimate biomass using the length/mass relationships of Towers et al. (1994). Where these were not sufficient, length/weight relationships were generated using individuals from samples or nearby sites. Crayfish were not included in biomass analyses as their occurrence was very patchy and a single individual in a sample had a disproportionate effect.

Functional organisation

Invertebrate trophic structure was described using functional feeding groups. This technique groups species together based on similar feeding characteristics. The groups used in this analysis are broadly those of Merritt & Cummins (1996). Species were divided into: browsers (predominantly consume algae), collector-filterers (filter material from the

flow using constructed nets), collector-gatherers (feed on organic deposits on the streambed), filter-feeders (filter material from the flow using mouthparts), predators (feed on other invertebrate species), and shredders (feed on coarse organic material e.g., leaves, wood). Trophic structure was described in terms of the number of species and the percentage of the total biomass in each trophic grouping. Filter-feeders were grouped with collector-filterers for the species composition analysis as there were very low numbers of collector-filterer species.

Food-web structure

Food-webs were described using the methods outlined in Jaarsma et al. (1998) and Thompson & Townsend (1999). Ten individuals of each animal taxon were used for gut analysis. Where 10 individuals were not available, as many individuals as possible were used. Although 10 individuals may be considered minimal, this represents a logistically challenging but achievable sample size for food-webs as rich in species as those considered here. Woodward & Hildrew (2001) found that large numbers of individual guts (100+) need to be surveyed to detect all trophic links, but such an effort was not feasible. Instead we have taken the approach of standardising effort across the different streams and taxonomic groups to make the food-webs comparable (Thompson & Townsend 2001). Ten individuals of each animal taxon per stream were selected to represent the full size range present. These individuals were processed for gut analysis either separately (for large invertebrates) or in groups of up to five (for smaller invertebrates) as described elsewhere (Jaarsma et al. 1998; Townsend et al. 1998). Invertebrates were gutted and the contents filtered onto 0.45 µm filters. These were mounted onto permanent slides and then read at 200–400× magnification. The species identity of gut contents was determined under a stereomicroscope, using a reference collection of invertebrate and algal taxa or relevant texts cited earlier. This technique allowed identification of most contents to either species or genus level for both animal and algal taxa. Algal taxa that were found in gut contents but not in rock scrubblings were added to the list of algal taxa present. Terrestrial invertebrates in the gut were grouped into a single basal category. Unidentifiable material was either classified as organic detritus and included as a single basal category, or as inorganic material and excluded from the food-web.

Food-web attributes were calculated using the methods described in Jaarsma et al. (1998). Numbers

of species, links and food chains, mean chain lengths (Pimm 1982), and the numbers of top, intermediate, and basal species were extracted using an Excel® macro (Jaarsma et al. 1998). Connectance and prey:predator ratios were calculated using the formulae from Jaarsma et al. (1998).

Statistical analyses

Similarity percentages (Clarke & Warwick 1994) in invertebrate species lists between sites and land-use types were calculated based on biomass data, using the Simper procedure in Primer (Plymouth Marine Laboratory). Species were chosen as discriminators if the ratio of the average dissimilarity between land-use groups to the standard deviation of the dissimilarities exceeded 2, and if the contribution of the species to the overall biomass exceeded 1%.

Land-use differences in physico-chemical parameters and food-web structure were tested using one-factor analysis of variance, or where assumptions of normality were violated, Kruskal-Wallis tests (Systat 9.0, SPSS Inc. 1999). Location of significant differences were tested using Tukey's post-hoc tests for ANOVA, and Dunn's test for Kruskal-Wallis. Relationships between the sites in terms of both distribution of biomass across species and food-web structure were displayed using multi-dimensional scaling (MDS) ordinations (Clarke & Warwick 1994). Land-use differences in multivariate data were tested by means of analysis of similarities (ANOSIM) (Clarke & Warwick 1994) with 10 000 iterations ($\alpha = 0.05$). This procedure is analogous to ANOVA in univariate statistics and analyses whether the dissimilarities within our *a priori* defined groupings (i.e., land use) are higher than between groupings.

RESULTS

Physico-chemistry and algal productivity

Land use was related to physical characteristics of the streams, with tussock streams tending to be wider than pine streams of the same order (Table 1). Variability among sites in terms of depth, substrate size, and current speed was considerable, but did not vary consistently with land use. There were also differences evident in physico-chemistry, with significant differences in pH and nitrate/nitrite concentrations (Table 2). Native forest sites had the highest pHs, but all sites were circumneutral to alkaline. There was no evidence of acidification associated with pine sites. Patterns in nitrate/nitrite

Table 1 Physical parameters of the study streams. (SD, standard deviation). Kruskal-Wallis tests for effects of land use are shown with significant values indicated in bold. Significant post-hoc comparisons (Dunns) are shown.

Catchment	Site	Code	Land use	Av. depth (cm)	Av. width (m)	Av. substrate (mm)	Av. current (cm/s)
Lee	Blackrock	Brk	Pasture (P)	13.50	1.20	57.43	16.17
Lee	Broad	Brd	Pasture (P)	15.90	1.18	34.75	11.85
Lee	Canton	Can	Pasture (P)	20.30	1.25	81.19	11.04
Silver	North Col	NCl	Native forest (N)	11.00	2.61	91.29	2.56
Silver	Powder	Pdr	Native forest (N)	10.10	3.67	79.83	61.60
Meggathburn	Berwick	Ber	Pine forest (Ph)	9.60	0.55	39.00	12.60
Mimihau	Venlaw	Ven	Pine forest (Ph)	38.00	2.95	122.20	58.50
Akatore	Akatore A	AkA	Pine forest (Ph)	23.50	0.71	38.02	5.50
Akatore	Akatore B	AkB	Pine forest (Ph)	9.67	0.54	55.33	9.33
Craggy Tor	Catlins	Cat	Pine forest (Ph)	1.30	0.80	50.29	27.00
Narrowdale	Control	Con	Pine forest (Ph)	5.27	0.73	19.89	2.03
3 O’Clock	Dempsters	Dmp	Tussock (T)	22.00	3.72	118.93	6.63
Kye Burn	German	Ger	Tussock (T)	73.00	3.28	59.61	8.37
Kye Burn	Healy	Hly	Tussock (T)	15.80	3.03	96.75	9.61
Kye Burn	Kye Burn	KBn	Tussock (T)	6.50	1.97	122.02	4.39
Kye Burn	Little Kye	LKB	Tussock (T)	21.50	6.65	34.19	8.79
Sutton	Stony	Sty	Tussock (T)	14.10	2.85	182.63	11.78
Sutton	Sutton	Sut	Tussock (T)	11.60	2.40	106.22	7.05
Land-use effect:				2.61	10.80	4.45	2.61
P				0.46	0.01	0.22	0.46
Post-hoc tests				T>Pn			

Table 2 Water chemistry and food resources of the study streams. Nutrient concentrations are in µg/litre. (DRP, dissolved reactive phosphorus; AP, algal production; FPOM, fine particulate organic matter; CPOM, coarse particulate organic matter; AFDW, ash free dry weight.) One-factor ANOVA (*italics*) or Kruskal-Wallis tests for effects of land use are shown with significant values indicated in bold. Significant post-hoc comparisons (Tukeys, one-factor ANOVA; Dunns, Kruskal-Wallis) are shown.

Site	Land use	pH	Nitrate/ nitrite	NH ₃ -N	Total nitrogen	DRP	Total P	AP (mg C/m ² per h)	FPOM (g AFDW/m ²)	CPOM (g AFDW/m ²)	Biofilm (g AFDW/m ²)	Seston (mg AFDW/litre)
Brk	P	6.60	15.34	24.00	197.26	8.20	18.11	27.74	4.94	6.35	1.45	7.12
Brd	P	6.32	8.67	24.00	159.07	7.52	13.62	35.06	1.41	3.44	1.20	0.77
Can	P	6.68	16.80	18.00	199.08	7.86	21.38	23.04	2.89	8.56	1.95	4.59
NCl	N	7.16	67.28	9.00	279.09	5.64	11.63	0.32	4.34	26.87	3.51	5.02
Pdr	N	7.53	47.37	<0.01	164.53	9.06	20.10	3.85	4.46	34.35	9.14	1.16
Ber	Pn	6.96	597.86	2.47	811.70	31.43	43.23	9.62	19.79	65.73	1.84	1.08
Ven	Pn	7.12	33.08	14.02	178.16	6.28	17.83	7.28	3.90	9.35	7.31	1.99
AKA	Pn	6.84	403.86	22.05	648.13	10.34	19.28	14.64	17.51	205.98	2.03	2.65
AKB	Pn	6.92	278.13	24.12	575.15	122.29	163.38	9.45	8.13	130.20	1.47	3.87
Cat	Pn	7.10	60.55	<0.01	142.01	19.89	22.02	2.66	4.32	67.23	0.45	2.17
Con	Pn	6.72	80.82	58.38	401.30	38.37	58.99	4.01	10.53	20.31	1.26	2.22
Dmp	T	6.90	21.18	10.50	219.08	12.99	38.89	85.38	0.67	2.76	1.32	0.63
Ger	T	7.35	4.11	<0.01	88.15	2.05	8.42	88.29	0.34	0.41	2.29	1.07
Hly	T	6.94	7.28	<0.01	75.42	4.61	9.06	61.75	0.92	1.64	3.61	0.34
KBn	T	6.60	1.45	15.00	219.08	9.91	38.89	19.34	0.29	0.33	1.24	0.47
LKB	T	8.61	5.30	15.00	189.98	11.11	16.83	11.14	2.54	10.72	2.06	0.76
Sty	T	6.81	4.50	12.00	146.34	2.05	9.06	22.45	0.39	0.72	11.99	0.88
Sut	T	7.01	5.06	10.50	157.25	14.87	20.10	6.70	0.33	3.81	0.95	0.94
H _{2,17} / F _{3,14}	P	8.30	13.8	6.41	4.54	5.61	4.74	2.96	12.97	12.72	3.72	10.42
Post-hoc tests		<0.01 N>P	<0.01 Pn>T	0.09	0.21	0.13	0.19	0.07 Pn<T N<T	0.01 Pn>T	0.01 Pn>T	0.29	0.02 Pn>T

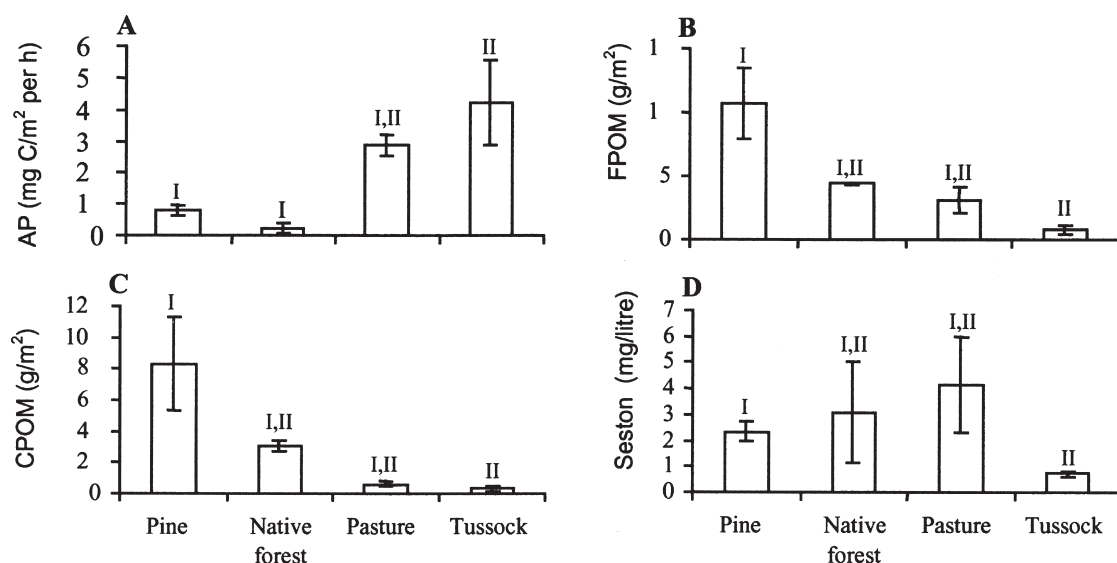


Fig. 1 Land-use differences in energy supply for **A**, algal production (AP); **B**, fine particulate organic matter (FPOM); **C**, coarse particulate organic matter (CPOM); and **D**, seston. Results are shown as means with standard error bars. Significant differences detected using post-hoc tests are indicated using different letters at the top of bars.

concentrations were particularly striking, with low concentrations in the tussock sites, intermediate concentrations in the pasture grassland sites and native forest sites, and very high concentrations in the pine forest sites (Table 1).

Differences in energy availability with land use were also evident. Grassland sites had significantly higher algal productivity than forested sites (Table 2), although one pine site (Berwick, 14.64 mg C/m² per h) was unusually productive (and also nitrate/nitrite enriched). A gradient of algal productivity exists from native forest sites through pine and pasture sites to tussock sites (Fig. 1A). Post-hoc tests (Table 2) reveal significant differences between pine sites and tussock sites, although low power means that differences between native forest sites and other sites were not significant. Despite differences in algal productivity, there were no significant differences in biofilm biomass between land uses. As expected, forested sites had more organic matter on the streambed (both as fine and coarse components) although pasture streams also retained substantial amounts of fine material (Fig. 1B,C). Seston at base flow was low in the tussock sites and high in two of the pasture sites, and in the native and pine forest sites (Fig. 1D). High variability and low power meant that post-hoc tests could only detect significant differences between the pine and the tussock sites.

Species composition and invertebrate biomass

Significant differences in species richness were observed among the land uses (Tables 3 and 4). More species were found in pasture and tussock sites compared with pine and native forest sites, mainly as a result of greater algal species richness in the grassland sites. Few fish species were present, but tussock sites tended to have more fish species. In terms of functional feeding groups, pine sites had more filter-feeder, collector-filterer, and shredder species. In keeping with previous studies (Friberg & Winterbourn 1997; Townsend et al. 1997), we found considerable overlap in species composition between different land uses, with 27 out of 129 taxa occurring in all four land-use classifications and 99 taxa occurring in more than one land use. Similarity percentages (Table 5) showed that sites in the two grassland categories overlapped more with each other than with forested sites, and pine forest sites overlapped least with any other category. Similarities between sites within land uses were relatively high, although pine sites were more variable, perhaps reflecting the greater geographical spread of these sites.

There were significant land-use effects on overall invertebrate biomass (Tables 3 and 4) with grassland sites supporting higher biomass than forested sites. A group of core taxa dominated the biomass in all sites (the browsing mayfly *Deleatidium* spp., the

Table 3 Food-web attributes. (S, species richness; Alg, algae; Br, browser; FF, filter-feeder; CF, collector-filterer; Cg, collector-gatherer; Om, omnivore; Sh, shredder; Pr, predator; C, connectance; L, number of trophic links; MCL, mean chain length; P:P, prey to predator ratio; IB, invertebrate (inv.) biomass in grams of ash free dry weight/m².)

Site: Land use:	Brk		Brd		Can	NCL		Pdr	AkA		AkB		Ber		Cat		Con		Ven		Dmp		Ger		Hly		KBN		LKB		Sty		Sut	
	P		P		P	N	N	N	Pn		Pn		Pn		Pn		Pn		Pn		T		T		T		T		T		T		T	
Total S	83		89		100		70		77		82		58		45		76		66		96		79		90		93		67		104		89	
Alg S	45		49		52		22		29		39		26		11		26		28		46		46		43		53		37		59		55	
Fish S	1		1		1		1		1		1		0		1		1		1		4		2		2		3		1		1		1	
Inv. S	37		39		47		47		47		42		31		33		49		37		46		31		45		37		29		44		33	
Br S	10		11		11		10		12		8		5		7		11		7		15		5		11		10		6		10		10	
FF+CF S	3		2		2		2		1		4		2		3		2		3		3		1		2		1		1		2		2	
Cg S	8		9		13		15		14		12		13		9		18		8		11		13		14		13		10		12		8	
Om S	4		3		6		2		3		5		0		2		2		2		2		4		3		3		3		3		1	
Sh S	4		4		4		5		4		6		5		7		8		7		2		2		2		3		2		6		2	
Pr S	8		10		11		13		13		7		6		5		8		10		13		6		13		7		7		11		10	
C	0.13		0.17		0.14		0.11		0.08		0.07		0.08		0.07		0.06		0.08		0.18		0.13		0.14		0.18		0.15		0.17		0.17	
L	375		565		708		421		268		224		117		110		155		187		966		353		589		629		375		832		423	
L/S	4.31		5.95		6.50		5.40		3.44		2.67		2.02		2.24		2.18		2.71		9.03		4.10		6.14		6.42		4.81		7.36		4.60	
MCL	2.24		2.25		2.45		2.27		2.24		1.61		1.72		1.57		1.69		2.12		4.42		2.40		3.02		2.35		2.39		2.38		1.79	
P:P	1.92		1.75		1.48		0.94		1.17		1.22		1.35		0.74		0.89		1.26		1.65		2.00		1.55		2.05		1.78		1.88		3.30	
IB	4.74		5.35		3.85		0.74		1.00		0.18		0.25		0.52		0.58		0.42		4.00		2.52		3.36		1.07		2.96		1.70		1.74	
% Br	62.20		57.68		28.53		45.71		42.85		16.47		18.73		13.56		13.22		19.79		31.67		10.80		6.85		20.68		34.63		34.20		62.62	
% Cf	0.35		0.00		1.64		0.26		6.19		0.00		0.00		0.00		0.14		0.00		1.07		0.20		0.19		4.60		0.23		0.09		1.29	
% Cg	33.17		27.00		56.80		19.59		20.90		18.34		58.13		9.27		6.22		5.24		38.30		63.57		66.23		52.12		51.46		22.79		4.81	
% FF+CF	0.86		2.59		0.85		0.50		1.60		12.52		21.36		0.01		0.38		0.72		2.79		4.21		8.08		6.46		1.38		10.12		9.09	
% Om	0.03		0.15		3.86		0.89		1.97		0.57		1.85		0.00		0.40		0.45		0.25		0.26		0.00		0.00		0.79		16.83		16.55	
% Sh	2.15		0.60		1.71		25.05		9.20		38.30		44.37		11.80		55.20		15.79		1.72		4.80		6.24		2.86		7.66		6.97		1.83	
% Pr	1.24		11.98		6.62		8.00		17.29		13.79		22.56		12.43		2.04		15.91		24.20		16.17		12.40		13.28		3.86		9.00		3.81	

Table 4 Results of one-factor ANOVA (italics) or Kruskal-Wallis tests for effects of land use are shown with significant values indicated in bold. Significant post-hoc comparisons (Tukeys, one-factor ANOVA; Dunns, Kruskal-Wallis) are shown. (P, pasture; Pn, pine; N, native forest; T, tussock.)

Attribute	$H_{2,17}/F_{3,14}$	<i>P</i>	Post-hoc tests
Total no. species (S)	<i>6.07</i>	0.01	<i>P</i> > Pn, T>Pn
No. algal	<i>12.05</i>	<0.01	<i>P</i> > N, <i>P</i> > Pn, T>N, T>Pn
No. fish	<i>7.48</i>	0.11	T>Pn
No. invertebrate	<i>0.23</i>	0.79	
No. browser	<i>1.38</i>	0.29	
No. collector-filterer			
+ filter-feeder	<i>4.29</i>	0.04	Pn>N
No. collector gatherer	<i>0.31</i>	0.74	
No. omnivores	<i>5.37</i>	0.15	
No. shredders	<i>13.36</i>	<0.01	Pn>P, Pn>N, Pn>T
No. predators	<i>0.24</i>	0.79	
Connectance	<i>31.80</i>	<0.01	<i>P</i> > N, <i>P</i> > Pn, T>N, T>Pn
No. trophic links (L)	<i>7.28</i>	<0.01	T>Pn, <i>P</i> > Pn
Links per species (L/S)	<i>8.97</i>	<0.01	T>Pn, <i>P</i> > Pn
Mean chain length	<i>11.73</i>	<0.01	T>Pn
Prey:predator ratio	<i>6.50</i>	0.01	
Invertebrate biomass	<i>14.72</i>	<0.01	T>Pn, <i>P</i> > Pn
% browser	<i>4.59</i>	0.02	<i>P</i> > Pn
% collector-filterer	<i>9.45</i>	0.02	
% collector-gatherer	<i>1.80</i>	0.19	
% filter-feeder	<i>0.87</i>	0.48	
% omnivores	<i>1.66</i>	0.65	
% shredders	<i>14.05</i>	<0.01	T<Pn, <i>P</i> < Pn
% predators	<i>0.57</i>	0.64	

Table 5 Similarity percentages generated by Primer showing similarity in species lists (presence/absence data) within and between land-use types.

	Pasture	Native forest	Pine	Tussock
Pasture	59.71			
Native forest	41.44	59.87		
Pine	34.59	43.25	45.72	
Tussock	50.61	38.67	29.53	50.05

elmid beetle *Hydora nitida*, and chironomids in the genus *Eukiefferiella*). However, distinctive assemblages of other species characterised the different land-use types. In particular, the dobsonfly *Archicauliodes diversus* was the dominant large invertebrate predator in grassland streams, whereas in forested settings it was the stonefly *Stenoperla prasinia*. A number of chironomid species were also strongly associated with grassland settings. The presence of other assemblages appeared to be a function of their functional feeding group.

Functional organisation

Forested sites had similar assemblages dominated by species feeding on coarse particulate organic matter (shredders) whereas grassland sites were characterised by species feeding on algae (browsers) or fine particulate organic matter (collector-gatherers). In particular, the shredding species *Rhabdomastrix* and *Austroperla cyrene*, as well as a suite of amphipod species, were strongly associated with forested sites. In contrast the grazing snail *Potamopyrgus antipodarum* was often absent from those sites, and the

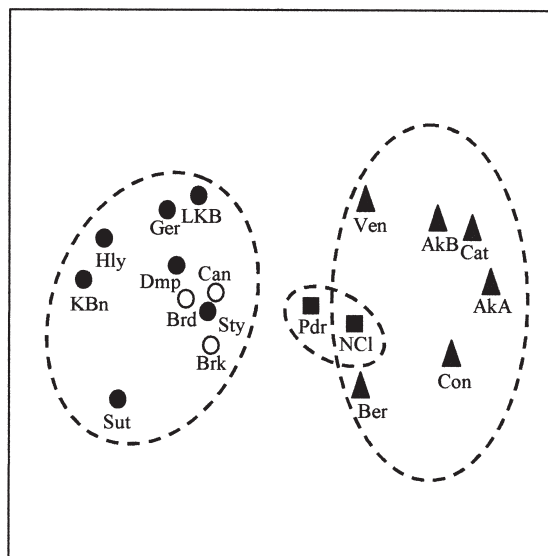


Fig. 2 Multi-dimensional scaling ordination of sites using distribution of biomass by invertebrate species. Statistically different groups (identified by analysis of similarities) are identified by dashed ellipses. (\blacktriangle , pine forest sites; \blacksquare , native forest sites; \bullet , tussock sites; \circ , pasture grassland sites.) For site codes see Table 1. Stress = 0.12.

biomass of the mayfly genus *Deleatidium* tended to be much lower. Differences in percentage of biomass in each functional feeding group were significant for shredders and collector-filterers, and approached significance for browsing species (Table 4). The separation of forest and grassland sites was clearly evident in an ordination of sites using biomass distribution across species (Fig. 2). A highly significant land-use effect was indicated using analysis of similarities ($R = 0.673$, $P < 0.01$).

Food-web structure

Grassland sites were distinguished by having more trophic links overall and per species (Table 3), and higher ratios of prey to predators, reflecting the large number of algal species in the food-webs. Grassland sites were also more highly connected internally and more structurally complex (Fig. 3A), whereas forested food-webs were characterised by simple food chains usually originating with detritus or plant material (in pine sites, predominantly pine pollen) (Fig. 3B). Food chain length was significantly shorter in the forested than the grassland sites and particularly short in pine streams (Table 3). An ordination of sites using food-web attributes (Fig. 4) distinguishes clusters representing forested sites and

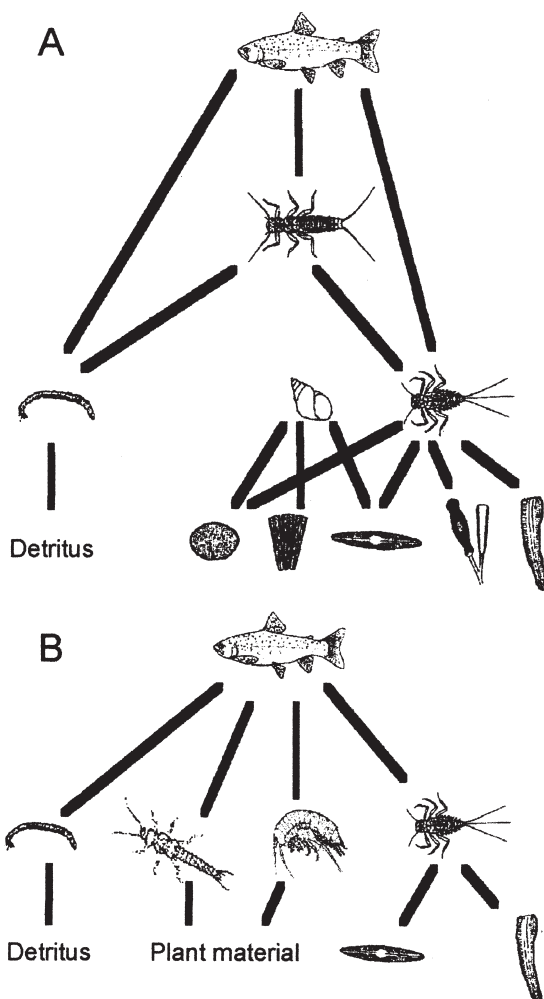


Fig. 3 Simplified representation of food-webs from **A**, a grassland stream (Kye Burn); and **B**, a forested stream (North Col). Each invertebrate and diatom species shown represents 10 in the real food-web. Most common trophic links are shown. Grassland food-webs are typified by more algal species and longer food chains, with most food chains being based on algal productivity. Forested food-webs are typified by short food chains based on detritus and plant material.

grassland sites. Analysis of similarities revealed a significant effect of land use (Global $R = 0.673$, $P < 0.01$), but no significant difference between pine and native forest or tussock and pasture sites.

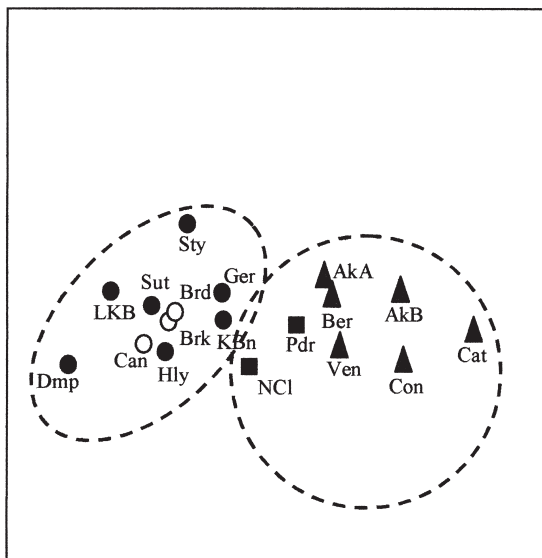


Fig. 4 Multi-dimensional scaling ordination of sites using food-web attributes (see Table 3). Statistically different groups (identified by analysis of similarities) are identified by dashed ellipses. (▲, pine forest sites; ■, native forest sites, ●, tussock sites; ○ pasture grassland sites.) For site codes see Table 1. Stress = 0.03.

DISCUSSION

Analysis of connectivity food-webs offers ecologists a compromise between simple structural representations of communities (e.g., species lists) and more rigorous and difficult functional and bioenergetic representations. The trend in recent years has been to introduce greater detail into food-webs (e.g., Lancaster & Robertson 1995), of which the detailed quantitative food-web of Benke & Wallace (1997) provides an extreme example. This study shows that with reasonable effort and replication, and a rigorous attempt to standardise methods, food-webs can be practically used to examine the relationships between environmental factors and community structure.

A number of variables were found to co-vary with land use. Although land-use change has also been shown to result in physical changes in channel shape (Davies-Colley 1997) and sediment dynamics (Leeks 1992), the streams in this study showed few consistent effects of land use on physical structure. However, the observation that tussock streams were wider than pine streams was broadly consistent with the results of Davies-Colley (1997). We did not observe the stream acidification associated with

conifer afforestation overseas (Ventura & Harper 1996), and so did not need to control for this factor in our study. However, there was some evidence of differences in water chemistry that could not readily be accounted for by land use alone. Nitrate values for the grassland sites are in keeping with those observed in other studies in the area (Townsend et al. 1998; Biggs et al. 2000). However, the concentrations in the pine sites were extremely high. This may reflect a combination of an underlying geological origin for nitrogen (Thompson et al. 2001) and low rates of nitrate uptake because of light limitation of algal productivity.

In common with previous studies we found that streams in forested landscapes displayed lower algal productivity than those in open settings (Hill et al. 1995; Rier & King 1996). Our sites showed a clear algal productivity gradient from native forest streams (lowest) through pine and pasture streams to tussock streams. The opposite pattern was seen in standing crop of organic matter, with a clear gradient from pine (highest) through native forest and pasture to tussock streams.

Each food-web had a "generalist core" of invertebrate species as is typical of New Zealand streams (Rounick & Winterbourn 1982; Harding & Winterbourn 1995), plus additional taxa that typified particular land-use types. In common with earlier work (Townsend et al. 1997a), this study found evidence for a distinctive shredder-based community in forested streams and an algal consumer-based community in the grassland streams. Like Friberg et al. (1997) we found high densities of amphipods in our pine streams, where they appeared to be functioning as important shredders of both needles and wood. This study found much larger differences in the representation of functional feeding groups between the pine sites and the other land uses than did Townsend et al. (1997a), probably reflecting the greater age and canopy cover of the pine trees in the current study. Harding & Winterbourn (1995) and Townsend et al. (1997a) observed the same patterns as this study in the occurrence of some predator species in certain land uses (the stonefly *Stenoperla prasinia* dominates forested streams, whereas the dobsonfly *Archicaultiodes diversus* dominates grassland streams). It is possible that the different nature of the primary consumers in the community may affect which predator species are dominant. For instance the presence of snails may favour *Archicaultiodes* (which is larger and more able to access this resource). Alternatively, the nature of the terrestrial vegetation may directly impact on the

stream fauna through effects on later stages of invertebrate life cycles (Collier et al. 1997).

Of particular note were significant differences in invertebrate biomass with land use. Tussock, pasture, and native forest streams all supported a higher biomass of invertebrates than pine streams. Friberg et al. (1997) showed higher invertebrate densities in open (i.e., grassland) as opposed to forested (native and pine) sites in New Zealand but found no difference between native forest and pine forest. This may be partly because of the presence of native plant species in the riparian zone of some of Friberg et al.'s (1997) pine sites. Harding & Winterbourn (1995) reported higher invertebrate biomass in pine forest than pastoral settings in New Zealand, but the pastoral settings in their study were described as having little evident algal biomass whereas the streams in the current study had high algal productivity and biomass. Whiles & Wallace (1997) reported similar invertebrate biomass in North American streams in pine afforested and broadleaf catchments; however they also noted a predominance in pine forest sites of trichopteran shredder species, a group that is relatively depauperate in New Zealand. The very low biomass of invertebrates in the pine sites is consistent with a gradient in energy availability from algal production-based grassland stream food-webs, to native forest food-webs based on high quality organic detritus, to pine forest food-webs with low algal productivity and poor quality detritus (Albarino & Balseiro 2002).

It is important to recognise that there are possible confounding effects in the consideration of land-use patterns. We did not have an accurate measure of disturbance history for all sites in this study. Disturbance is known to be important in affecting community composition (Townsend et al. 1997b) and structuring food-webs (Townsend et al. 1998). All these streams were sampled after extended periods of base flow (>1 month) so immediate disturbance history is unlikely to be an important confounding variable. However, afforestation is known to reduce water yields from grassland catchments (Fahey & Jackson 1997) so it is conceivable that longer-term disturbance histories could differ with land use and so contribute to differences in fauna.

In addition to simple differences in the invertebrate communities between the forested and grassland streams, there were profound land-use effects on food-web structure. The food-webs described here share many of the structural characteristics observed in food-webs before; food chains are short (Lawton 1989), omnivores, cannibals, and food

chain loops are rare (Pimm 1982; Cohen et al. 1990), and higher connectance was observed in the larger food-webs (Winemiller 1989; Cohen et al. 1990). In addition there is clear evidence of variation in food-web structure based on differences in riparian land use. Grassland food-webs had more algal species, displayed greater internal connectance, and had longer food chains. Forest food-webs, in contrast, tended to be based on detritus, with a simple food-web structure dominated by short food chains and with low prey:predator ratios, patterns that have also been described in detritus-based food-webs from an Ontario stream (Tavares-Cromar & Williams 1996). Some differences in food-web attributes are straightforward consequences of moving from algal-based to detritus-based food-webs. Whereas it is possible to identify separate algal species, detritus is most commonly left as a single amorphous grouping, so it is to be expected that links per species will be lower in a system dominated by detritivores. Other attributes however, such as connectance, food chain length, and species richness of invertebrates, should be independent of these artifacts of food-web description.

These results have significance when considered in a context of land-use change in New Zealand. Grassland streams and forested streams have distinctive assemblages of stream invertebrates that contribute towards biodiversity values. Land-use change in riparian margins that converts grassland to forested settings (such as occurs during afforestation of tussock grassland by exotic conifer species) can be expected to have profound effects on stream communities. This is an important (and ongoing) impact on grassland systems, where gully areas which have not been converted from native grassland to exotic pasture are now being planted for forestry purposes. This change is likely to have fundamental effects on stream food-webs. Equally, deforestation from harvest can be expected to influence stream food-webs. It would be expected that after harvest, stream communities would alter to more closely resemble those found in grassland settings. Protection of aquatic habitats requires an holistic approach that considers aquatic communities in the context of riparian land use.

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The food-webs used in the paper are available at: www.telperion.otago.ac.nz/erg/freshwater/online_data. Files may be used by permission of the author.

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