Small-scale patch complexity, benthic invertebrate colonisation and leaf breakdown in three headwater streams in Bay of Plenty, New Zealand

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RESEARCH ARTICLE

Small-scale patch complexity, benthic invertebrate colonisation and leaf breakdown in three headwater streams in Bay of Plenty, New Zealand

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We assessed the effects of patch complexity on benthic macroinvertebrate colonisation and leaf breakdown in three headwater streams in the Kaimai Range, New Zealand. We used three patch types: complex, disturbed, and unaltered control patches, and measured colonisation of macroinvertebrates and leaf breakdown rates within each patch. We hypothesised colonisation and breakdown would be highest in the complex patches and lowest in disturbed patches. With the exception of percentage of total shredders, no differences were found in macroinvertebrate diversity or community structure and no treatment effect was evident for leaf breakdown rates. While this may suggest no influence of patch complexity on leaf breakdown, we cannot discount unmeasured site-specific influences, such as a high flow event, which occurred during the treatment period, as clear differences were evident between the three streams. Higher spatiotemporal replication and more appropriate seasonal sampling would be required to further explore this relationship.

Keywords: allochthonous; ecosystem function; leaf litter; macroinvertebrate; New Zealand; patch dynamics

Introduction

Streams are inherently patchy, thus the patch dynamics concept of stream ecology underpinned much of the empirical research that followed its conception (Pringle et al. 1988; Townsend 1989). Townsend (1989, p. 47) penned 'every section of every streambed is patchy on some scale and has its own kinds of disturbances, colonisers, colonist sources, and species interactions'. Patches clearly influence the distribution and abundance of lotic organisms and can provide critical refugia for their persistence (Sedell et al. 1990; Lancaster & Hildrew 1993). Moreover, stream organisms have developed life history traits to respond to and exploit these patch-related phenomena (Townsend 1989).

One critical process in streams that operates in a patchy manner within the spatial mosaic of a stream benthos is leaf litter breakdown (Reice 1974). Leaf material entering streams often forms into clumped patches, dependent on flow–substrate interactions (Hoover et al. 2006), and this patchiness is likely also reflected in leaf litter quality variations. Allochthonous material is a critical component of forest stream food webs and, along with primary producers, forms the base of stream food webs in general (Kaushik & Hynes 1971; Wallace et al. 1997).

Leaf breakdown typically involves three key processes (Webster & Benfield 1986). Upon entering streams, leaves leach a significant proportion of

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their organic and inorganic material, and are then colonised and conditioned by microbes. Finally, fragmentation occurs through mechanical means and invertebrate processing (Webster & Benfield 1986). Each of these processes is dependent on, and mediated by, a variety of influences such as water chemistry and temperature, rates of physical abrasion, and the source pool of invertebrates (Petersen & Cummins 1974; Webster & Benfield 1986). It stands to reason, therefore, that rates of decomposition of this material vary in response to many external influences and stressors at each stage of the process, such as land use (Paul et al. 2006), acid mine drainage (Hogsden & Harding 2013), acidification (Dangles et al. 2004), nutrients (Woodward et al. 2012), and forest disturbance (Lecerf & Richardson 2010). However, leaf breakdown typically occurs at a faster rate when there is a greater abundance of shredding invertebrates present (Jonsson et al. 2001; Sponseller & Benfield 2001; Young et al. 2008), but is often dependent on preceding microbial activity to condition leaves (Cummins et al. 1989, Graca 2001), and can also depend on the composition of leaf litter (Swan & Palmer 2006). Consequently, leaf breakdown is considered a fundamental part of stream ecosystem functioning (Gessner & Chauvet 2002; Young et al. 2008), and is often used as an index of ecosystem function (Young et al. 2008; Young & Collier 2009; Niyogi et al. 2013).

Leaf litter breakdown has been well studied in New Zealand streams for a variety of reasons. Much of this work has focused on comparing breakdown and invertebrate colonisation of different leaf species (e.g. Linklater 1995), including studies that have found little difference in invertebrate preferences of native and exotic leaves (e.g. Parkyn & Winterbourn 1997; Hicks & Laboyrie 1999; Quinn et al. 2000). Typically, breakdown in these studies has been driven predominantly by the activity of a small number of shredder species, such as the caddisfly *Olinga*. New Zealand streams are characterised by their paucity of shredders, resulting from a predominantly evergreen flora and aseasonal supply of allochthonous input (Winterbourn et al. 1981; Thompson & Townsend 2000). Nevertheless, to our knowledge, no study has specifically focused on the influence of patch complexity on leaf colonisation and breakdown in New Zealand streams.

The variability of leaf breakdown within stream riffles (Tiegs et al. 2009), led us to assess the influence of small-scale patch complexity on this fundamental process. To explore the effects of patch complexity on colonisation of benthic macroinvertebrates and corresponding leaf breakdown, we took a small-scale patch manipulation approach. Specifically, we manipulated benthic habitat patches at small spatial scales, using three different patch types (control, disturbed and complex), and assessed the effect on benthic macroinvertebrate colonisation and associated leaf breakdown in three New Zealand headwater streams. We hypothesised that macroinvertebrate colonisation and leaf breakdown would be highest in the complex patches as a result of increased habitat availability and lowest in the disturbed patches. Despite the paucity of shredders in New Zealand streams, we hypothesised that this increased leaf breakdown would be a result of increased shredder density colonising leaf packs given the winter sampling and assumed lower influence of temperature and microbes. Where macroinvertebrates were excluded from leaf breakdown processes (using fine mesh bags), we expected to observe a subsequent reduction in leaf litter breakdown.

Materials and methods

Study sites

We ran this experiment in three streams draining the eastern slopes of the Kaimai Range into Tauranga Harbour, Bay of Plenty, New Zealand (Fig. 1). Te Poupou Stream (hereafter referred to as stream AB1) is a third-order tributary of Aongatete River, with riparian vegetation consisting of primarily native forest and scrub. Te Rereatukahia Stream (AB2) is a fourth-order stream with primarily native forest and scrub in the riparian zone. Boyd Stream (AB3) is a second-order tributary of the Uretara Stream with riparian vegetation consisting of mostly native scrub and some scattered *Pinus radiata*. AB1 and AB2 are situated within the
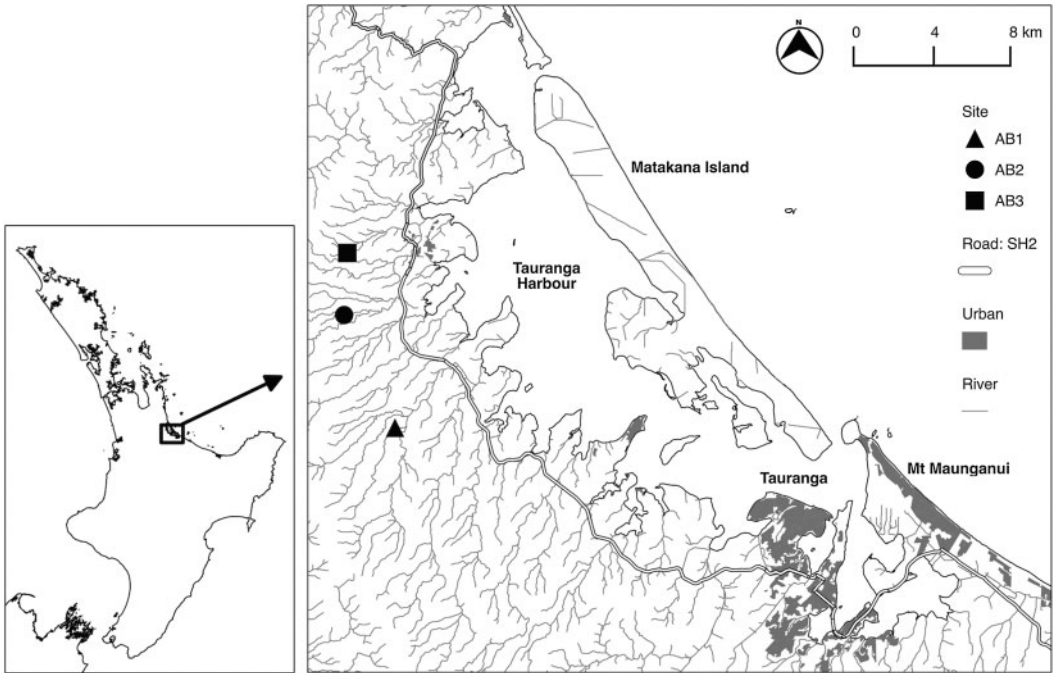
Figure 1 Map showing location of three study streams in eastern Bay of Plenty, New Zealand.

Kaimai Forest Park, whereas AB3 is situated downstream of the park boundary and drains a section of cattle and sheep and beef farming, as well as some scattered avocado orchards, but predominantly flows through native forest.

Experimental design

To assess leaf litter breakdown and macroinvertebrate colonisation in relation to patch complexity, we used three patch type treatments: complex, disturbed and control. To ensure independence of replicate patches within riffles, we chose a patch size of 0.25 m² and located patches 3 m apart. Each patch type was replicated five times each per stream. Thus, each stream had 15 individual patches.

Mussel spat rope has recently proven effective at assisting fish and shrimp passage through stream culverts by altering flow dynamics and increasing structural complexity (David & Hamer 2012; Tonkin et al. 2012; David et al. 2014. For a demonstration of their complexity and habitat provision for a freshwater shrimp, see http://dx. doi.org/10.6084/m9.figshare.694255). Given these properties, in addition to their strength and longevity, we used mussel spat rope to increase structural complexity and created complex patches by arranging a 3 m length of mussel spat rope ('Mega Loop spat rope', Quality Equipment Group Ltd., Auckland, New Zealand) within the 0.25 m² patch. We attached the mussel rope to the streambed with 40 cm steel pegs hammered into the substrate. The disturbed treatment patch was created by thoroughly scrubbing the substrate in situ with a wire brush until it was bare at the beginning of the trial period. The depth of disturbance depended on the embeddedness of the benthos: up to a depth of approximately 20 cm. The control treatment patch was left unmodified.

Sampling

Leaf bags

We used mahoe (*Melicytus ramiflorus*) to assess leaf breakdown, due to the minimal fragmentation that occurs during the breakdown process. To reduce

inconsistencies, we picked mahoe leaves from numerous trees within close proximity and air dried leaves for several weeks in a cool, dry environment. We used two kinds of leaf litter bags (15×10 cm): a coarse mesh, 8 mm aperture, to allow macroinvertebrate access and stiff plastic to reduce scouring; and a fine mesh bag, 500 µm aperture, which excluded macroinvertebrate colonisation.

For extracting after 30 d, we filled 45 each of coarse and fine mesh bags with c. 3 g dry weight of mahoe leaves. For extracting after 15 d, we filled a further 45 coarse bags with c. 1.5 g of leaves. We weighed leaves using electronic scales to the nearest thousandth of a gramme and we labelled each bag with metal tags.

We secured three leaf bags (one 30 d fine mesh bag and two 15 and 30 d coarse mesh bags; see sample preparation details below) with 40 cm steel pegs and galvanised wire in the middle of each patch. Leaf bags lay flat on the substrate in the direction of water flow. The two 30 g bags (one fine and one coarse mesh) were attached together, and the additional coarse bag (1.5 g) was attached separately to enable removal after 15 d.

Forty-five bags were deployed in c. 70 m reach of each stream, 135 bags in total for the study. The 45 bags containing 1.5 g of leaves were intended to be collected from streams after 15 d with the remaining 90 bags retrieved after 30 d. Bags were removed carefully to retain leaf litter and macroinvertebrates and placed in individual zip-lock bags for transport to the laboratory for processing.

Physicochemical characteristics and substrate variables

We conducted all fieldwork between 6 July and 8 August 2012. We spot-measured dissolved oxygen using an OxyGuard Handy Polaris meter (OxyGuard International A/S, Birkerød, Denmark), and conductivity and temperature around midday at each site using a Eutech Instruments ECTestr 11 meter (Eutech Instruments, Singapore).

We measured substrate composition using the 'Wolman Walk' technique (Wolman 1954), which involves categorising the β-axis of 100 randomly-chosen stones whilst walking at 45° to the bank

along a zig-zag transect. The proportion of each Wentworth scale substrate size, expressed as a percentage, was multiplied by the middle value of that category. These amounts were summed and divided by the total number of samples, to produce a single substrate size index value representative of the stream site from which they were taken.

We visually estimated percentage canopy cover for each reach and categorised riparian vegetation cover classes (native forest, pasture, etc). We measured channel widths at three points along the study reach and depth at five different points along the thalweg. Current velocities were also taken using the velocity head rod method (Wilm & Storey 1944) at the same five points.

Macroinvertebrates and periphyton biomass

To characterise benthic macroinvertebrate communities in each of the three study streams, we collected five 0.1 m^2 Surber (500 µm mesh) samples randomly from riffles in each study reach at the beginning of the experimental period. We preserved samples in 70% ethanol and identified them in the laboratory to the lowest possible taxonomic level using available keys (Towns & Peters 1996; Winterbourn et al. 2000).

We calculated macroinvertebrate density (individuals 0.1 m^{-2}), number of taxa and Simpson's diversity index ($1- \lambda$'; Simpson 1949) to summarise different aspects of diversity. These metrics were the mean values calculated for the five individual samples at each site. We calculated the number and percentages of the different functional feeding groups (FFGs): scrapers; deposit feeders; predators; and shredders. We also calculated the number and percentage of total shredders; those that were either primary or secondary shredders. Primary shredders are species with a primary feeding habit of coarse organic matter consumption, whereas secondary shredders are more facultative in their consumption of leaf material. Nonetheless, it is important to note here that shredders are particularly underrepresented in New Zealand streams and there are no obligate shredders, with browsers predominating (Winterbourn et al. 1981).

At each macroinvertebrate sample location, we collected a stone (five total) for chlorophyll-*a* analysis, used as an estimate of periphyton biomass. Stones were kept cool in the dark before being frozen. We extracted chlorophyll-*a* using 90% acetone at 5 °C for 24 h in the dark and read absorbances on a Varian Cary 50 conc UV-Visible Spectrophotometer (Varian Australia Pty Ltd, Mulgrave, Australia) and converted these to pigment concentration following Steinman & Lamberti (1996). We estimated stone surface area according to Graham et al. (1988) and then halved this value to account for the proportion of the stone available for periphyton growth.

Leaf processing

We processed leaf bags on the day they were collected from the field. Individual bags were rinsed of sediment and sorted to separate leaves and macroinvertebrates in the laboratory. Any macroinvertebrates found were preserved in 70% ethanol for later identification. Damp leaves from individual bags were placed with their metal identification tags into a tin foil pouch and placed on oven trays in rows and dried at 30 °C for 72 h. Leaves were rotated within their pouches daily and their position was also regularly changed. Once dried to a consistent weight, the leaves were again weighed using electronic scales to the nearest thousandth of a gramme. Leaf mass loss was calculated as the percentage of weight lost over the sampling period. As we were only interested in comparing between patches, with the same leaf species and over the exact same time period, we did not use the exponential decay model (Petersen & Cummins 1974). Further, given the importance of temperature on leaf breakdown and the fact we did not log temperature through the study period, between-stream differences could not be comprehensively assessed.

Statistical analyses

To assess differences among treatments for leaf mass loss and macroinvertebrate metrics, we used randomised block analysis of variance (ANOVA) using the 'aov' function, with stream as the blocking factor. For the 30 d leaf breakdown percentage ANOVA, we included both fine and coarse mesh leaf bags, and thus included a treatment × bag type interaction in the model to assess if treatment influenced breakdown rates between fine and coarse mesh bags.

To visualise the multivariate structure of macroinvertebrate communities between streams and treatments, we used non-metric multidimensional scaling ordination, with the 'metaMDS' function in the Vegan package (Oksanen et al. 2011). We used presence/absence data and pooled invertebrate data for the five Surber samples at each site and also pooled leaf bag data for each treatment at each site.

To assess whether macroinvertebrate communities taken from Surber samples were different between the three streams, we used one-way PERMANOVA with the 'adonis' function in the Vegan package, using 999 permutations. Further, we used a two-way PERMANOVA, without interaction, to assess differences in macroinvertebrate assemblages colonising leaf bags between treatments and streams. For this test, we also ran a one-way PERMANOVA with sites treated as strata (blocks), which constrains permutations. However, this produced a similar outcome to the two-way model; thus, we only present the two-way results to indicate the importance of site differences.

We used Pearson's correlation to assess whether any macroinvertebrate metrics, or individual taxon abundances, were linked with leaf breakdown rates using the 'rcorr' function in the package Hmisc (Harrell Jr 2014). We corrected for false discovery rate (Benjamini & Hochberg 1995) using the 'p. adjust' function and 'fdr' method in the 'stats' package ($\alpha = 0.05$). All analyses were performed using R version 2.15.2 (R Core Team 2013).

Results

Physicochemical variables and periphyton biomass

All three study streams were relatively cool (c. 10 °C around midday) and highly saturated (> 110% dissolved oxygen). Study streams ranged from 3 m

to 7.5 m wide, 17 cm to 29 cm deep, and had mean water velocities of 0.43 m s^{-1} to 0.84 m s^{-1}. Stream AB3 was shallower, narrower, less stable, had lower velocity, and had smaller substrate and more fine sediment than AB1 and AB2 (Table 1). Periphyton biomass, assessed as chlorophyll-*a*, averaged 0.62 μg cm^{-2}, but did not differ between the three streams (Table 1; Fig. 2).

Macroinvertebrates: benthos

A total of 40 taxa were collected from the benthos in the three streams, with 27 at AB1, 26 at AB2 and 22 at AB3. Trichoptera (AB1: 9; AB2: 11; AB3: 9) was the most taxonomically rich group across the three streams, followed by Ephemeroptera (AB1: 6; AB2: 4; AB3: 7) and Diptera (AB1: 6; AB2: 5; AB3: 1). The most common species, present in all three streams, were the tipulid *Aphrophila neozelandica*, the cased caddisflies *Beraeoptera roria*, and two species of *Pycnocentria*, and the net-spinning caddisfly *Aoteapsyche colonica*, as well as lesser numbers of the leptophlebiid mayfly *Deleatidium* sp. and cased caddisfly *Olinga feredayi*.

The number of individuals found in the benthos averaged 30.73 per 0.1 m^2 across the three streams. Density was four times higher at AB2 than

AB1 (Tukey's HSD: $P = 0.036$) and seven times higher than AB3 (Tukey's HSD: $P = 0.018$), but there was no difference between AB1 and AB3 (Tukey's HSD: $P = 0.93$; Table 1; Fig. 2). Taxonomic richness averaged 9.47 taxa per 0.1 m^2, but there was no difference in the number of taxa between the three stream sites, nor was there a difference in Simpson's diversity index (Table 1; Fig. 2), which averaged 0.81.

Benthic macroinvertebrate communities differed between the three sites (PERMANOVA: $F_{2,12} = 2.30$, $P = 0.003$). No particular groups of taxa contributed strongly to these differences, with communities at sites AB1 and AB3 being predominantly nested subsets of those present at site AB2. Scrapers were the most numerically dominant and taxonomically rich functional feeding group (FFG) across the three stream sites with 90% composition and 21 taxa at AB1, 94.9% composition and 20 taxa at AB2, and 80.9% composition and 18 taxa at AB3 (Fig. 2). Other FFGs represented less than 10% of composition of benthic macroinvertebrates at all sites with the exception of predators at AB3, which represented 14.9% composition (Fig. 2). However, several of these taxa have shared or secondary feeding patterns, including shredding. The majority of these taxa were

Table 1 Mean (± 1 SE) physicochemical variables and macroinvertebrate metrics sampled at three streams (AB1–AB3) in the Kaimai Range, Bay of Plenty, New Zealand, July–August 2012.

Variable	N	AB1	AB2	AB3	$F_{2, 12}$	P
Chlorophyll-*a* (μg cm^{-2})	5	0.92 (0.44)	0.89 (0.27)	0.06 (0.04)	2.63	0.113
Density (No. 0.1 m^{-2})	5	16.00 (4.18)	66.80 (21.29)	9.40 (1.57)	6.25	0.014
No. of taxa (0.1 m^{-2})	5	9.00 (1.64)	12.60 (2.32)	6.80 (1.16)	2.74	0.105
Simpson's diversity	5	0.82 (0.04)	0.82 (0.06)	0.80 (0.03)	0.04	0.964
Depth (cm)	5	26.2 (3.1)	29.4 (2.9)	17 (0.9)	–	–
Width (m)	3	5.5 (0.6)	7.5 (0.5)	3.0 (0.3)	–	–
Velocity (m s^{-1})	5	0.76 (0.09)	0.84 (0.08)	0.43 (0.05)	–	–
Temperature (°C)	1	11.1	9.3	11.1	–	–
Conductivity (μS cm^{-1})	1	50	60	60	–	–
Dissolved oxygen (%)	1	111	113	112	–	–
Substrate embeddedness	1	Moderate	Moderate	Loose	–	–
Substrate size index	1	79	148	50	–	–

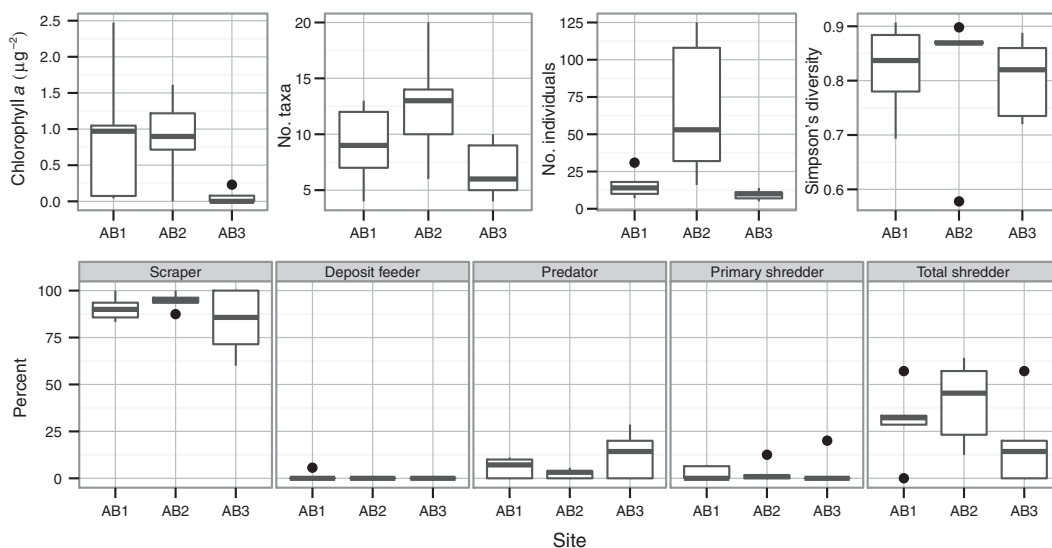AB1, Te Poupou Stream; AB2, Te Rereatukahia Stream; AB3, Boyd Stream.

Figure 2 Boxplots displaying mean chlorophyll-*a*, number of taxa, number of individuals and Simpson's diversity index values for benthic macroinvertebrates at three streams (AB1–AB3) in the Kaimai Range, Bay of Plenty, New Zealand, July–August 2012. Bottom panel displays percent composition of main functional feeding groups for each of these streams. Note: primary shredders are those that are considered to primarily be shredders, whereas total shredders comprise taxa with both primary and secondary preferences for shredding. AB1, Te Poupou Stream; AB2, Te Rereatukahia Stream; AB3, Boyd Stream.

primarily scrapers, such as the caddisflies *Olinga* and *Pycnocentria*, and stonefly *Zelandobius*. When considering taxa that are both primary and secondary shredders, AB1 had eight taxa comprising 30% of animals in the benthos, AB2 had nine that made up 39.4% composition, and AB3 had only three taxa comprising 17% of animals (Fig. 2).

Macroinvertebrates: leaf bags

Of the 135 total deployed bags, 25 were not retrieved due to a high-flow event during the treatment period in which bags were either dislodged from the substrate and lost downstream or buried under deposited sediment.

Fewer taxa were collected from leaf bags than the benthos, with 28 being collected across the three streams, and these were largely a subset of benthic samples. There was no difference in richness, density, or Simpson's diversity for the invertebrates present in leaf bags between streams or treatments (Table 2; Fig. 3). However, the number and percent of total shredders colonising leaf bags

differed between the three streams, and the percentage of total shredders was significantly lower in disturbed than control patches (Tukey's HSD: $P = 0.04$; Table 2; Fig. 3). Macroinvertebrates colonising leaf bags did not differ between treatments ($F_{2,29} = 0.72$, $P = 0.73$), but differed between the three streams (PERMANOVA: $F_{2,29} = 6.22$, $P = 0.001$; Fig. 4).

Leaf breakdown

No difference was found in breakdown rates between the three treatment patches (complex, disturbed and control) in any of the bag settings or streams (Table 3; Fig. 5). Differences between the three streams outweighed any treatment effect. This was evident for all the bag configurations (i.e. 15 and 30 d coarse mesh, and 30 d fine mesh bags). These differences were mostly between AB3 and the remaining two sites (Fig. 5).

Leaf breakdown averaged 50.98% (±1.33%) loss in the 30 d coarse mesh bags and ranged between 29.59% and 62.98% loss. Breakdown was

Table 2 Results of randomised block ANOVA of macroinvertebrate metrics from 30 d coarse leaf bags. Treatments were complex, disturbed and control patches in three streams (AB1–AB3) in the Kaimai Range, Bay of Plenty, New Zealand, July–August 2012.

Factor	F	P
(a) Richness		
Treatment	0.52	0.600
Stream (block)	0.10	0.901
(b) No. individuals		
Treatment	0.30	0.747
Stream (block)	0.80	0.459
(c) Simpson's diversity index		
Treatment	1.01	0.374
Stream (block)	0.77	0.472
(d) Total no. shredders		
Treatment	2.33	0.115
Stream (block)	5.37	0.010
(e) % Total shredders		
Treatment	3.45	0.045
Stream (block)	4.83	0.016

AB1, Te Poupou Stream; AB2, Te Rereatukahia Stream; AB3, Boyd Stream. Degrees of freedom for all factors were 2, 29.

significantly higher at AB1 (56.71% ± 1.4%; Tukey's HSD: $P < 0.0001$) and AB2 (55.57% ± 1.74%; Tukey's HSD: $P < 0.0001$) than AB3 (44.48% ± 1.43%), but there was no difference between AB1 and AB2 (Tukey's HSD: $P = 0.917$). Breakdown in fine mesh bags was slightly lower overall than the coarse mesh, but this was not significantly different (48.64% ± 2.28%; min = 19.09%; max = 73.54%). Again, AB1 (55.88% ± 1.76%; Tukey's HSD: $P < 0.0001$) and AB2 (61.5% ± 2.48%; Tukey's HSD: $P < 0.0001$) exhibited much greater breakdown than AB3 (35.23% ± 1.53%), but no difference was evident between AB1 and AB2 (Tukey's HSD: $P = 0.186$).

None of the leaf bag macroinvertebrate metrics (number of individuals, richness, Simpson's diversity index, total number of shredders, percentage shredders) were correlated with leaf mass loss ($P > 0.05$), nor were any of the individual taxon abundances found in leaf bags, after correcting for false discovery rate ($P > 0.05$).

Discussion

Patch complexity

Little evidence was found of the effect of patch complexity on either macroinvertebrate colonisation or leaf breakdown in these three streams. The only factor to be influenced by patch complexity was the percentage of combined shredders, which were lower in disturbed patches than control, but with no difference in complex patches. Contrary to our hypothesis, this did not convert into a functional response in terms of altered leaf breakdown. Moreover, no macroinvertebrate metric or individual taxon was correlated with leaf breakdown rates.

During the treatment period, there was a high-flow event that may have affected the results and somewhat homogenised treatment responses. Twenty-five of the original 135 bags were either lost downstream or buried. Some loss or burial of bags is to be expected under normal conditions, but this is a relatively high proportion suggesting some effect of the flow event. Nonetheless, streams AB1 and AB2 had relatively stable streambeds, with little substrate turnover likely. As with most processes, disturbance occurs within lotic systems in a highly patchy manner (Reice 1985; Townsend et al. 1997), both creating and destroying patches (Lake 2000), and the importance of bed stability for benthic invertebrate diversity is well understood (Schwendel et al. 2012; Tonkin & Death 2012; Tonkin et al. 2013). However, while leaf breakdown has been assessed in response to low-flow disturbance, where little effect was found (Death et al. 2009), assessing its response to high-flow disturbance regimes has not specifically been studied to our knowledge. From this, we can infer that some scouring effects may have also occurred on leaves during the high-flow event, especially in the coarse bags, although we did use thick plastic material to reduce scouring effects. Abrasion of leaves in coarse mesh bags can result in leaf fragmentation that could result in an overestimation of breakdown and be incorrectly attributed to chemical and biological inputs (Young et al. 2008).
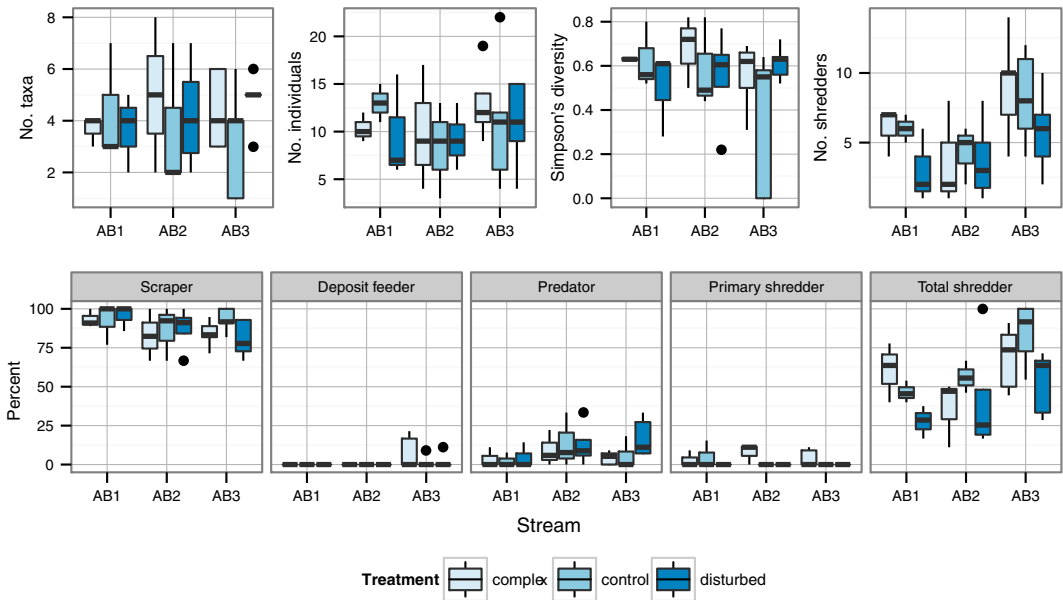
Figure 3 Boxplots displaying mean number of taxa, number of individuals, Simpson's diversity index and total number of shredder macroinvertebrates in 30 d coarse leaf packs at three streams (AB1–AB3) in the Kaimai Range, Bay of Plenty, New Zealand, July–August 2012. Bottom panel displays percent composition of main functional feeding groups for each of these streams. Note: primary shredders are those that are considered to primarily be shredders, whereas total shredders comprise taxa with both primary and secondary preferences for shredding. AB1, Te Poupou Stream; AB2, Te Rereatukahia Stream; AB3, Boyd Stream. Complex, light blue; control, medium blue; disturbed, dark blue.

Several other possibilities exist for the lack of treatment effect in the present study. One may be that the patches were too small to instigate a strong treatment effect. The highest variability in leaf breakdown has been found within stream riffles compared to broader scales in stream networks (Tiegs et al. 2009). Although stream invertebrates have been found to respond to within-stream patches using experimental approaches previously (Palmer et al. 2000), small instream experimental studies can be hampered by this site-specific response (e.g. Tonkin & Death 2013). If a true lack of treatment response applies here, it is noteworthy in itself and opposes our primary hypothesis, suggesting small-scale patch complexity does not alter leaf breakdown rates.

It is also possible that shredder activity was too low to have an influence given the time of year and species pool. Other than *Polypedilum*, shredders or secondary shredders were not common in leaf bags at any stream, with the stonefly

Zelandobius sp. and two *Pycnocentria* caddisflies being the next most common, both of which are also considered secondary shredders. In comparison to elsewhere, there is a paucity of shredders in New Zealand's stream macroinvertebrate communities due to the evergreen nature of the flora and associated aseasonality of the food supply (Winterbourn et al. 1981, Thompson & Townsend 2000). Furthermore, this study was performed during winter months and thus water temperatures were low, likely slowing the rate of breakdown. With the highest percentage of leaf mass lost being 74%, perhaps greater effects could have been extrapolated with a longer treatment period.

Stream effects

As found with previous studies (Robinson et al. 1998, Collier et al. 2006), our results showed highly site-specific leaf breakdown dynamics. The
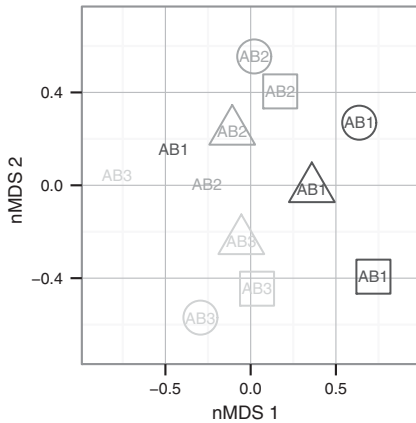
Figure 4 Non-metric multidimensional scaling (nMDS) ordination of benthic macroinvertebrates using presence/absence data in three streams (AB1–AB3) in the Kaimai Range, Bay of Plenty, New Zealand, July–August 2012. Plot displays pooled data for benthic samples and pooled data for 30 d coarse leaf bags deployed at three treatment patches. Circles, control; squares, complex; triangles, disturbed; no shape, benthic. AB1, Te Poupou Stream (dark); AB2, Te Rereatukahia Stream (medium); AB3, Boyd Stream (light). Stress = 0.17.

Table 3 Results of randomised block ANOVA of leaf breakdown percentages using (a) 15 d coarse mesh bags and (b) 30 d fine and coarse mesh bags, including treatment × bag type interaction. Treatments were complex, disturbed and control patches in three streams (AB1–AB3) in the Kaimai Range, Bay of Plenty, New Zealand, July–August 2012.

Factor	d.f.	F	P
(a) 15 d coarse			
Treatment	2, 36	0.25	0.782
Stream (block)	2, 36	13.93	<0.0001
(b) 30 d combined			
Treatment	2, 61	0.50	0.610
Bag type	1, 61	2.15	0.148
Stream (block)	2, 61	60.98	<0.0001
Treatment x bag type	2, 61	1.46	0.241

AB1, Te Poupou Stream; AB2, Te Rereatukahia Stream; AB3, Boyd Stream. Bag type represents either fine or coarse mesh bags.

higher macroinvertebrate densities and richness in the benthos at AB2 did not translate into corresponding breakdown rates for leaves compared to AB1. Though breakdown rates for leaves were lower at stream AB3, which aligns with the lower macroinvertebrate richness and total and shredder densities in the benthos, the actual densities of invertebrates in bags at two of the three treatments were higher than at the other streams. Rather than being used solely as a food source, leaf packs can also provide habitat or refuge for invertebrates (e.g. in glacial streams; Robinson et al. 1998). The limited habitat for benthic macroinvertebrates at AB3, with less riffle habitat and smaller substrate size compared to the other two streams, indicates this may have occurred in the present study. In fact, while measured physicochemical characteristics were largely the same between the three streams, the difference in habitat at AB3 was reflected in the more dissimilar benthic samples compared to the other two sites, as well as compared to AB3 leaf bags. Contrary to AB1

and AB2, leaf packs at site AB3 comprised somewhat different taxa to those of the benthos. This was largely driven by the chironomid *Polypedium* spp., which was overwhelmingly the most common taxon in leaf packs, but was not present in any benthic samples. Furthermore, greater presence of fine sediment at AB3 may also have lowered leaf breakdown rates through sediment accrual inside the bags (Dangles et al. 2001).

AB3 was the only stream sampled that passed through agricultural landscape, which is usually associated with higher instream nutrient concentrations. This enrichment, in conjunction with higher water temperatures, can stimulate microbial action causing increased breakdown of organic matter (Young et al. 1994; Paul et al. 2006), but results vary as the effects of land use can have confounding effects on breakdown processes (Hagen et al. 2006) with non-linear responses commonly observed (Young & Collier 2009; Woodward et al. 2012). High natural variability occurs in breakdown within heterogeneous bio-geo-climatic regions, but within homogeneous regions it should be possible to detect changes (Jesús Casas et al. 2011). While leaf breakdown can be sensitive to factors such as forest disturbance, it may require
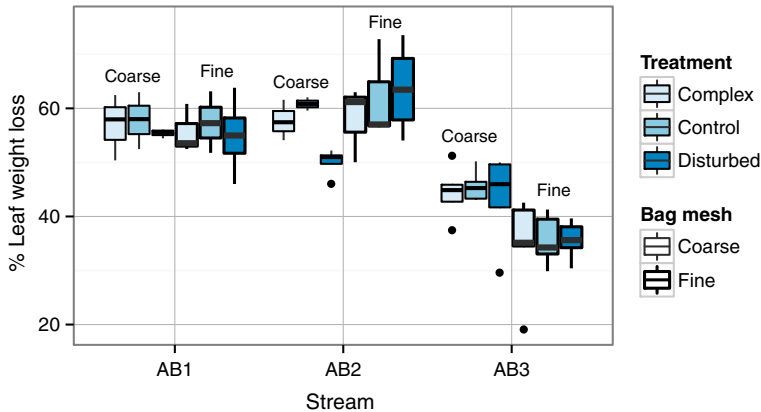
Figure 5 Boxplot displaying total percent weight loss of 30 d leaf packs in three streams (AB1–AB3) in the Kaimai Range, Bay of Plenty, New Zealand, July–August 2012. AB1, Te Poupou Stream; AB2, Te Rereatukahia Stream; AB3, Boyd Stream.

more than minor changes to detect a noticeable effect (Lecerf & Richardson 2010), and the large majority of this stream runs through native forest with intact riparian vegetation downstream of the forest boundary.

Coarse mesh bags allow colonisation of macro-invertebrates, which should lead to greater break-down rates (Wright & Covich 2005) particularly in unimpaired streams where shredder activity is often higher (Sponseller & Benfield 2001) compared to degraded sites where microbial activity may dom-inate breakdown (Young et al. 2008). Therefore, we hypothesised, but did not find, greater breakdown consistently in coarse bags. As previously high-lighted, the lack of difference between bag types may in part reflect lower shredder activity during the experimental period. Nevertheless, while shred-ders can account for a substantial proportion of decomposition in streams (Hieber & Gessner 2002), microbial action is critical for this process in lotic environments (Baldy et al. 1995; Pascoal & Cássio 2004; Duarte et al. 2006), and shredders preferentially select leaves that have already been exposed to, and conditioned by, microbial action (Graca 2001). In some cases, although apparently not in this study, fine-mesh bags can allow small early instar organisms to contribute to greater breakdown rates. This underlines the importance

of incorporating alternative mesh types into experi-ments so that an appraisal of the comparative influence of invertebrate and microbial activity can be judged (Gessner & Chauvet 2002).

Conclusions

With the exception of percentage of total shredders, no differences were found in macroinvertebrate diversity or community structure between the three patch complexity treatments, indicating little to no effect of patch manipulation on macroinvertebrate colonisation. Likewise, no treatment effect was evident for leaf breakdown rates. Differences in macroinvertebrates, both sampled from the benthos and colonising leaves, and leaf breakdown rates were more evident between the three streams. No treatment effect may suggest a lack of patch complexity influence on leaf processing rates at these small spatial scales. However, we cannot discount unmeasured site-specific influences such as physicochemical conditions. Further, the high flow event during the 30 d treatment period probably differentially influenced breakdown between streams. We suggest that higher spatiotem-poral replication and more appropriate season selection would be required to further explore this patch–function relationship.

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